SAS

THE JOURNAL OF POMOLOGY AND HORTICULTURAL SCIENCE

Vol. XVII

1939

HEADLEY BROTHERS

109 Kingsway, London, W.C.2

England

PRINTED AND MADE IN GREAT BRITAIN BY HEADLEY BROTHERS, ASHFORD, KENT

TABLE OF CONTENTS

JOURNAL OF POMOLOGY, Vol. XVII

No. 1 (March, 1939)

PAGE

The influence of the intermediate in double worked apple trees: Nursery trials of the "stem-builder" process at East Malling. By N. H. Grubb 1

The influence of "stem-builder" intermediates on apple root systems. By W. S. Rogers, A. Beryl Beakbane and Carol P. Field 20

On the occurrence and spread of the Ring Spot disease of lettuce caused by *Marssonina panattoniana* (Berl.) Magn. By Greta B. Stevenson 27

Incompatibility and sterility in the Gage and dessert plums. By M. B. Crane and A. G. Brown 51

Root Studies VII. A survey of the literature on root growth, with special reference to hardy fruit plants. By W. S. Rogers .. 67

No. 2 (June, 1939)

On the quantities of nitrogen, phosphoric acid, potash and lime removed from the soil by a crop of Roscoff broccoli during its growth. By E. Vanstone and C. E. H. Knapman 85

Root Studies VIII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors. By W. S. Rogers 99

Root Studies IX. The effect of light on growing apple roots: A trial with root observation boxes. By W. S. Rogers 131

Anatomical studies of stems and roots of hardy fruit trees. II. The internal structure of the roots of some vigorous and some dwarfing apple rootstocks, and the correlation of structure with vigour. By A. Beryl Beakbane and Eleanor C. Thompson 141

Magnesium-deficiency of fruit trees. By T. Wallace 150

Effects of variation in the supply of potash to lettuces grown under glass. By R. M. Woodman 167

Book Reviews 181

No. 3 (September, 1939)

PAGE

The influence of size on the dry matter, mineral, and nitrogen content of hyacinth bulbs. By J. Hargrave and F. C. Thompson .. 185

On the use of chlorinated nitrobenzenes for the control of Club Root disease of Brassicae. By Margaret J. Smieton 195

Developmental studies in the apple fruit in the varieties McIntosh Red and Wagener. I. Vascular anatomy. By Mary MacArthur and R. H. Wetmore 218

Seasonal variations of starch content in the genus Rosa, and their relation to propagation by stem cuttings. By Dorothy Brandon 233

Studies on the nutrition of tulips and Narcissi. By C. Bould .. 254

Nutrient uptake by the tomato plant. By A. H. Lewis and F. B. Marmoy 275

Physiological breakdown in stored Monarch plums. By W. H. Smith 284

Book Review 292

No. 4 (January, 1940)

Editorial Notice 293

E. A. Bunyard. An appreciation 294

The effects of a deficiency of certain essential elements on the development and yield of carrots, onions and radishes grown in sand cultures under glass. By R. M. Woodman 297

Field sampling for the comparison of infestations of strawberry crops by the aphis *Capitophorus fragariae* Theob. By R. M. Greenslade and S. C. Pearce 308

Mosaic disease of the raspberry in Great Britain. II. Experiments in transmission and symptom analysis. By R. V. Harris .. 318

Water-culture studies with apple trees. II. The seasonal absorption of nitrogen and potassium by Cox's Orange Pippin on Malling rootstocks Nos. IX and XII. By H. L. Pearse .. 344

The incorporation of growth hormones in seed dressings. By H. E. Croxall and L. Ogilvie 362

Book Reviews 385

INDEX

JOURNAL OF POMOLOGY, Vol. XVII

APPLE : PAGE

ANATOMICAL STUDIES : of stems and roots of hardy fruit trees. II. The internal structure of the roots of some vigorous and some dwarfing apple rootstocks, and the correlation of structure with vigour. By A. Beryl Beakbane and Eleanor C. Thompson 141

DEVELOPMENTAL STUDIES in the apple fruit in the varieties McIntosh Red and Wagener. I. Vascular anatomy. By Mary MacArthur and R. H. Wetmore 218

NUTRITION : Magnesium deficiency of fruit trees. By T. Wallace 150

Water-culture studies with apple trees. II. The seasonal absorption of nitrogen and potassium by Cox's Orange Pippin on Malling rootstocks Nos. IX and XII. By H. L. Pearse 344

ROOTSTOCKS AND INTERMEDIATES : The influence of the intermediate in double worked apple trees : Nursery trials of the " stem-builder " process at East Malling. By N. H. Grubb 1

The influence of " stem-builder " intermediates on apple root systems. By W. S. Rogers, A. Beryl Beakbane and Carol P. Field 20

Apple root growth in relation to rootstock, soil, season and climatic factors. By W. S. Rogers. 99

BEAKBANE, A. BERYL and THOMPSON, ELEANOR C. Anatomical studies of stems and roots of hardy fruit trees. II. The internal structure of the roots of some vigorous and some dwarfing apple rootstocks and the correlation of structure with vigour 141

BEAKBANE, A. BERYL. See Rogers, Beakbane and Field.

BOOK REVIEWS :

The genetics of garden plants. By M. B. Crane and W. J. C. Lawrence. (J.L.F.) 181

Scientific Horticulture. *The Journal of the Horticultural Education Association.* Vol. VII, 1939. (R.H.S.) 182

Statistical methods for research workers. By R. A. Fisher. (T.N.H.) .. 183

Diseases of stone fruits and hops. By H. Wormald (G.S.) 183

Commercial fruit tree spraying. Methods and costs. By J. Turnbull. (Hubert Martin) 292

Fundamentals of fruit production. By V. R. Gardner, F. C. Bradford, and R. D. Hooker (R. H. Stoughton) 388

Fruit growing. Modern cultural methods. Edited by N. B. Bagenal. (C.E.H.) 390

Fruit juices and related products. By V. L. S. Charley and T. H. Harrison. (B.T.P.B.) 385

Plant hormones and their practical importance in horticulture. By H. L. Pearse. (M.A.H.T.) 387

BOULD, C. . Studies on the nutrition of tulips and Narcissi 254

BRANDON, DOROTHY. Seasonal variations of starch content in the the genus Rosa, and their relation to propagation by stem cuttings 233

PAGE

BROWN, A. G. See Crane and Brown.

BULBS : The influence of size on the dry matter, mineral and nitrogen content of hyacinth . . . By J. Hargrave and F. C. Thompson 185

CARROTS : The effects of a deficiency of certain essential elements on the development and yield of . . . onions and radishes grown in sand cultures under glass. By R. M. Woodman 297

CLUB ROOT DISEASE OF BRASSICAE : On the use of chlorinated nitrobenzenes for the control of . . . By Margaret J. Smieton 195

CRANE, M. B. and BROWN, A. G. Incompatibility and sterility in the Gage and dessert plums 51

CROXALL, H. E. and OGILVIE, L. The incorporation of growth hormones in seed dressings 362

FIELD, CAROL P. See Rogers, Beakbane and Field.

GREENSLADE, R. M. and PEARCE, S. C. Field sampling for the comparison of infestations of strawberry crops by the aphis *Capitophorus fragariae* Theob. 308

GRUBB, N. H. The influence of the intermediate in double worked apple trees : Nursery trials of the " stem-builder " process at East Malling 1

HARGRAVE, J. and THOMPSON, F. C. The influence of size on the dry matter, mineral and nitrogen content of hyacinth bulbs 185

HARRIS, R. V. Mosaic disease of the raspberry in Great Britain. II. Experiments in transmission and symptom analysis 318

HORMONES : The incorporation of growth . . . in seed dressings. By H. E. Croxall and L. Ogilvie 362

INCOMPATIBILITY and sterility in the Gage and dessert plums. By M. B. Crane and A. G. Brown 51

KNAPMAN, C. E. H. See Vanstone and Knapman.

LETTUCE : On the occurrence and spread of the Ring Spot disease of . . . caused by *Marssonina panattoniana* (Berl.) Magn. By Greta B. Stevenson.. 27

Effects of variation in the supply of potash to lettuce grown under glass. By R. M. Woodman 167

LEWIS, A. H. and MARMOY, F. B. Nutrient uptake by the tomato plant .. 275

MACARTHUR, MARY and WETMORE, R. H. Developmental studies in the apple fruit in the varieties McIntosh Red and Wagener. I. Vascular anatomy. 218

MARMOY, F. B. See Lewis and Marmoy.

MOSAIC DISEASE of the raspberry in Great Britain. II. Experiments in transmission and symptoms analysis. By R. V. Harris. 318

NUTRITION : On the quantities of nitrogen, phosphoric acid, potash and lime removed from the soil by a crop of Roscoff broccoli during its growth. By E. Vanstone and C. E. H. Knapman 85

Magnesium-deficiency of fruit trees. By T. Wallace 150

Effects of variation in the supply of potash to lettuces grown under glass. By R. M. Woodman 167

Studies on the nutrition of tulips and Narcissi. By C. Bould 254

Nutrient uptake by the tomato plant. By A. H. Lewis and F. B. Marmoy 275

The effects of a deficiency of certain essential elements on the development and yield of carrots, onions and radishes grown in sand cultures under glass. By R. M. Woodman 297

Water-culture studies with apple trees. II. The seasonal absorption of nitrogen and potassium by Cox's Orange Pippin on Malling rootstocks Nos. IX and XII. By H. L. Pearse 344

PAGE

OGILVIE, L. See Croxall and Ogilvie.

ONIONS: See under Carrots.

PEARCE, S. C. See Greenslade and Pearce.

PEARSE, H. L. Water-culture studies with apple trees. II. The seasonal absorption of nitrogen and potassium by Cox's Orange Pippin on Malling rootstocks Nos. IX and XII 344

PLUM: Incompatibility and sterility in the Gage and dessert plums. By M. B. Crane and A. G. Brown 51

Physiological breakdown in stored Monarch plums. By W. H. Smith .. 284

PROPAGATION: Seasonal variations of starch content in the genus Rosa, and their relation to propagation by stem cuttings. By Dorothy Brandon 233

RADISHES. See under Carrots.

RASPBERRY: Mosaic disease of the . . . in Great Britain. II. Experiments in transmission and symptom analysis. By R. V. Harris .. 318

ROGERS, W. S., BEAKBANE, A. BERYL and FIELD, CAROL P. The influence of "stem-builder" intermediates on apple root systems 20

ROGERS, W. S. Root Studies. VII. A survey of the literature on root growth with special reference to hardy fruit plants 67

Root Studies. VIII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors 99

Root Studies. IX. The effect of light on growing apple roots: A trial with root observation boxes 131

RING SPOT DISEASE: On the occurrence and spread of . . . of lettuce caused by *Marssonina panattoniana* (Berl.) Magn. By Greta B. Stevenson 27

ROOT STUDIES: VII. A survey of the literature on root growth with special reference to hardy fruit plants By W. S. Rogers 67

VIII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors. By W. S. Rogers 99

IX. The effect of light on growing apple roots: A trial with root observation boxes. By W. S. Rogers 131

ROSA: Seasonal variations of starch content in the genus . . . and their relation to propagation by stem cuttings. By Dorothy Brandon .. 233

SMIETON, MARGARET J. On the use of chlorinated nitrobenzenes for the control of Club Root disease of Brassicae 195

SMITH, W. H. Physiological breakdown in stored Monarch plums 284

STEVENSON, GRETA B. On the occurrence and spread of Ring Spot disease of lettuce caused by *Marssonina panattoniana* (Berl.) Magn. 27

STRAWBERRY APHIS (*Capitophorus fragariae* Theob.): Field sampling for the comparison of infestations of strawberry crops by the . . . By R. M. Greenslade and S. C. Pearce 308

THOMPSON, ELEANOR C. See Beakbane and Thompson.

THOMPSON, F. C. See Hargrave and Thompson.

TOMATO: Nutritional uptake of the . . . plant. By A. H. Lewis and F. B. Marmoy 275

PAGE

VANSTONE, E. and KNAPMAN, C. E. H. On the quantities of nitrogen, phosphoric acid, potash and lime removed from the soil by a crop of Roscoff broccoli during its growth 85

VEGETABLES:

DISEASES: On the use of chlorinated nitrobenzenes for the control of Club Root disease of Brassicae. By Margaret J. Smieton 195

On the occurrence and spread of the Ring Spot disease of lettuce caused by *Marssonina panattoniana* (Berl.) Magn. By Greta B. Stevenson .. 27

NUTRITION: Effects of variation in the supply of potash to lettuces grown under glass. By R. M. Woodman 167

On the quantities of nitrogen, phosphoric acid, potash and lime removed from the soil by a crop of Roscoff broccoli during its growth. By E. Vanstone and C. E. H. Knapman 85

The effects of a deficiency of certain essential elements on the development and yield of carrots, onions and radishes grown in sand cultures under glass. By R. M. Woodman 297

WALLACE, T.: Magnesium-deficiency of fruit trees 150

WETMORE, R. H. See MacArthur and Wetmore.

WOODMAN, R. M. Effects of variation in the supply of potash to lettuces grown under glass 167

The effects of a deficiency of certain essential elements in the development and yield of carrots, onions and radishes grown in sand cultures under glass 297

THE INFLUENCE OF THE INTERMEDIATE IN DOUBLE WORKED APPLE TREES:

NURSERY TRIALS OF THE "STEM-BUILDER" PROCESS AT EAST MALLING

By N. H. GRUBB
East Malling Research Station

I. Introduction.

Certain Continental nurserymen have for many years made a practice of double working standard apple trees on seedling stocks. It is claimed that trees with long stem-pieces of certain "stem-builder" varieties give the nurserymen three definite advantages. First, the stems of the trees are stouter than they would be if the stocks were "low-worked" with the variety to form the head. Secondly, the method produces a larger proportion of saleable standard trees on variable seedling stocks than could be obtained in the usual way. Thirdly, the heads are either larger, or are obtained in a shorter time, than would otherwise be possible.

From the East Malling viewpoint the most interesting of these claims is the second. It appears to imply that the variation in the influence of seedling rootstocks may, by the "stem-builder" process, be at least partially eliminated. Those who have seen blocks of nursery trees raised by this method have commented on their apparent uniformity; there seemed, in fact, to be enough evidence to justify a nursery trial of the method on a considerable scale. The present report deals with the results of such a trial, begun in 1931 and concluded in 1937.

The problem has been approached mainly from the point of view of rootstock influence and its possible modification by the use of intermediates in double working. For this no apology need be offered. Since rootstock influence has been for a quarter of a century the theme of a large part of the work at East Malling, any opportunity of obtaining fresh light on its nature, and on any factors which tend to modify it, cannot be allowed to pass. Evidence as to the validity of the other claims made for the "stem-builder" process is also presented; from the practical point of view this will undoubtedly be of some interest.

The Nurseryman's Viewpoint.

The additional expense of raising trees in this way must, of course, be considerable. Some Continental nurserymen have evidently found it justified;

and if their claims can be substantiated, this can readily be understood. Fruit growers might perhaps be prepared to pay more for trees with stouter stems, especially for the planting of orchards where the grass is kept short by grazing; the stouter stems would presumably reduce the time during which it is necessary to protect the trees from injury. The gains from the production of a larger proportion of saleable trees, or from larger heads, or their production in a shorter time, are obvious.

It may be questioned, however, whether British nurserymen would find the expense justified. The losses from trees which will not make saleable standards in a reasonable length of time are often less than might be expected, since in most nurseries such trees are cut back and made into saleable bush trees.

The Grower's Viewpoint.

But what is likely to be the attitude of the grower to this method of obtaining better results in the nursery? It will depend, of course, on the behaviour of the trees after they are planted out. Whilst there is at least a fair chance that the results may be generally satisfactory—the trees giving a uniformly high standard of performance—there are at least two other possibilities, either of which would be seriously to the grower's disadvantage.

In the first place, if the "stem-builder" intermediates make the tree more uniform in the nursery, this influence may persist, or it may be only temporary. If it is temporary, the proportion of trees which in the ordinary way would have been too weak to make standards in the nursery will show their weakness *after* planting out instead of before. In other words, the grower will be planting a larger instead of a smaller proportion of unsatisfactory trees.

Secondly, the grower has to reckon with the true influence of the intermediate. The East Malling trials of double worked apples and pears have failed to reveal a reliable method of forecasting the results of any particular combination of intermediate and second scion. In certain cases, vigorous varieties used as intermediates have eventually much dwarfed one or more of the second scion varieties worked on them. Furthermore, owing to the invigorating effect on the root system of the growth of the variety used as intermediate, this true dwarfing influence may not begin to appear until the second scion is three or four years old. For example, if Bramley had been used as a "stem-builder" in the production of standard trees of Cox's Orange, it would probably have served its purpose well enough *in the nursery*; but after planting out, the trees would soon have become weak and unsatisfactory.

It is impossible to say without trial whether the vigorous varieties used on the Continent as "stem-builders" will eventually invigorate or dwarf the second scions worked on them. It is at least possible that some of them may

invigorate one second scion variety and dwarf another. In any case, since they are all vigorous, any such dwarfing influence cannot be expected to appear for several years ; the grower will discover it, not the nurseryman.

Still further, the East Malling trials with double worked apple trees seem to show that a piece of intermediate two feet long exerts more influence than a piece three inches long. In the "stem-builder" process there will seldom be less than four or five feet of intermediate, which may conceivably increase the true influence still more.

The "stem-builder" process, then, *may* be quite harmless to the grower's interests. But there is at least a possibility that it may lead either to his planting a larger proportion of poor trees than usual, or to a uniformly *bad* performance of his trees. Clearly this Continental practice needed investigation. The present trial was designed primarily to throw further light on the nursery aspects of the problem, the trees being lifted and their weights recorded when the second scions had made three years' growth. A study of the behaviour of such trees as orchard standards would require a very much more extensive and long continued experiment.

2. Material and Arrangement.

Rootstocks.

Since one of the objects of the "stem-builder" process is to obtain an increased proportion of saleable trees on seedling stocks, it was obviously necessary to include in the trial a complete set of trees on such stocks. These were obtained from a trade source ; nothing is known about their origin.

In order to provide a further test of the influence of the "stem-builder" intermediates, it was decided to include also sets of trees on two vegetative rootstocks, one known to be dwarfing and the other vigorous. If the "stem-builder" intermediates reduce the variation in vigour of trees on variable seedling stocks, they should also bring trees on a dwarfing and vigorous stock closer together in vigour. The choice fell on the very dwarfing Jaune de Metz, No. IX, and the nameless very vigorous stock, Malling No. XII. These were obtained from the East Malling stool-beds ; both were from clonal selections.

Intermediates.

Three varieties used as "stem-builders" were obtained from a large nursery in South Germany. The names given were Noir de Vitry, Normanischer Ciderapfel and Gelber Trier'scher Weinapfel. Since none of these is well known, at least under these names, in Great Britain, they will be referred to in the following pages as A, B and C respectively. Each of the second scion varieties was also used as intermediate, reworked only with the same variety.

Second Scion Varieties.

In a nursery trial of this kind it was obviously important to select a second scion variety which is known to show very clearly the variable influence of seedling rootstocks. The variety eventually chosen was Early Victoria. As a contrast to this, it was decided to use Newton Wonder, which appears to vary on seedling stocks as little as any variety. Though these two varieties have largely lost their popularity as commercial apples, they served the purpose of this trial very well, and there is little reason to regret their choice.

The results of the trial suggest that they do differ in the degree to which they show rootstock influence. But since the second scion varieties were not treated identically throughout, one being pruned and the other left unpruned, this can be demonstrated only from the records of the intermediates.

Replications.

Each unit of 25 stocks was repeated three times. Since each second scion variety was worked on intermediates of itself, as well as of A, B and C, and there were three rootstocks, IX, XII and seedling, the total number of units was 72. The total number of stocks planted was 1,800 ; but owing to a few failures, there was never a complete set of 1,800 worked trees. The 72 units were arranged in " balanced blocks ".

Nursery Treatment.

The stocks were planted 15 inches apart in rows 4 feet apart, in February 1931. They were budded with the intermediate varieties in the summer of 1931, and the failures were grafted in the spring of 1932. In the following winter the remaining failures were removed. It is now realized that this was a mistake, more especially as the failures were irregularly distributed, and seem to have had little relation to either rootstock or scion variety. This point is discussed below.

The intermediates were " run up " as rapidly as possible for working standard high. After two years' growth, at the end of 1933, most of them were tall enough, the few exceptions being mainly, of course, amongst the trees on the dwarfing Jaune de Metz rootstock. In the spring of 1934 all that were tall enough were regrafted with the second scion variety as nearly as possible 5 feet above the top of the first scion. Those not tall enough were left in place, as were subsequently those whose second scions failed to grow.

There were no single worked trees in the trial. In a few cases, intermediates of Early Victoria and Newton Wonder were not tall enough for regrafting ; and in other cases the second scions failed to grow. But such trees were not strictly comparable with the trial trees.

Pruning.

In 1933 and 1934 the lateral shoots from the intermediates were kept short by pinching ; at the beginning of 1935 they were all removed, and the stems thereafter were kept free from laterals.

The second scions of Early Victoria were left unpruned throughout. Those of Newton Wonder were severely shortened in the spring of 1935, the beginning of their second year, but were left unpruned subsequently.

3. AVAILABLE RECORDS AND METHOD OF PRESENTATION.

The size of both the intermediates and the second scions at various stages was recorded as fully as time permitted. The records comprise the length of wood growth of the intermediates in each of the two years before they were regrafted, and of the second scion at the end of its first year's growth ; the stem size of both the intermediate and the second scion at the end of each of the three years' growth of the latter ; and, of the second scion only, the number of shoots (over 5 cm.) made in its second and third year's growth ; its weight at the conclusion of the trial ; the number of fruit buds and the number and weight of fruits borne ; and, for the last year only, the number of fruits infected with Scab. The weight of the intermediates at the conclusion of the trial is also in part available, and, for one unit of each treatment, the weight of the rootstocks with a measured length of roots.

Twenty-four trees were also excavated in detail, with their complete root systems. These, and the rootstock and intermediate weights just mentioned, are described and summarized by Rogers, Beakbane and Field in the paper which follows this.

In summarizing these records for presentation the writer has met with certain difficulties. In the first place, the removal, after one year's growth of the intermediates, of the stocks whose buds and grafts had failed is now seen to have been a mistake. It is quite clear that the trees next to a gap made by this removal had a better chance than those with neighbours on both sides ; they grew better, and produced more fruit buds and fruits, and usually larger fruits, freer from Scab infection. Nor is this all. The effect of the gaps was greatest where the trees were largest and therefore most liable to shade each other ; it was greater with both second scion varieties where the rootstock was No. XII or seedling than where it was No. IX ; and it was greater with Early Victoria (unpruned throughout) than with Newton Wonder (severely pruned at one year old).

It therefore becomes necessary to deal separately with the "crowded"*

* For the sake of brevity, the trees which had a neighbour at a distance of 15 inches on each side will be referred to as "crowded". It must be emphatically stated, however, that in current nursery practice, stocks for standard trees are usually planted even more closely than were those in the present trial.

trees and those next to gaps. Fortunately there were few units with less than six "crowded" trees. Of trees next to gaps there were frequently few, but always several where there was any shortage of "crowded" trees. It is therefore possible where necessary to supplement the data obtained from the "crowded" trees alone with those from the trees next to gaps.

The material provides two methods of approach to the main problem—the presumed effect of the "stem-builder" intermediates in "evening up" rootstock influence. There is first a comparison of the variation of the second scions on seedling stocks where the intermediate was a "stem-builder" with that where it was of the same variety as the second scion. And, secondly, there is a comparison of the differences between second scions on IX and XII where the "stem-builder" intermediates were present with those where they were not.

A second difficulty is met in the study of the variation amongst the trees on seedling stocks. The obvious method is to compare the coefficient of variation of the groups, for either size measurements, blossom and fruit counts, or the relationship between these two. The method is simple and straightforward; it is easy to show that by this criterion the "stem-builder" intermediates did apparently reduce the variation in size amongst the second scions, at least of Early Victoria. The difficulty arises in the attempt to interpret this result. It has become clear that the variation in size amongst large trees, as measured by the coefficient of variation, is usually less than amongst small trees of the same variety; the trees apparently become less variable as they grow larger. Now since the "stem-builder" intermediates, as will be obvious later (Table IV), have almost always invigorated the second scions, the reduced variation may be merely associated with the increased size of the trees.

It seems probable that in blossom and fruit bearing also, trees old enough to bear large numbers are apt to be less variable than young trees just beginning to bear (but an exception occurs, of course, where trees with a strong biennial habit are not all "in step"). In the present trial many of the trees on XII produced no fruit buds at all up to the time of the last record. In such a case, any mathematical expression of the variation amongst the trees becomes almost meaningless.

Amongst the trees on seedling stocks, however, the proportion without blossom was considerably smaller. Though the blossom and fruit counts themselves are not very serviceable, the relationship between blossom counts and wood growth is more hopeful. For this purpose, since wood growth measurements are not available after the first year of the second scions, use has been made of the percentage of shoots bearing terminal fruit buds.

Since the cause of the reduced variation in size of the trees on "stem-builder" intermediates is open to doubt, it was necessary to look for an

alternative method of examining the size data. It was observed that, where two years' records were available, certain individuals were above the average of their unit in one year and below it in the other. In other words, these individuals tend to "even up", and reduce the variation in the unit; they approach the average instead of receding from it, as do those individuals which are either above or below the average in both years. The proportion of such individuals should reveal any general tendency of the unit to become either more or less variable. There may, however, be certain complicating factors, of which the most obvious is biennial bearing, at least where the trees are not all "in step". In the present trial none of the trees on seedling stocks (or on XII) became noticeably biennial; this factor can therefore be ignored.

The presentation of the results obtained from the trees on IX and XII is not quite so straightforward, since it involves a comparison of comparisons. The method used is the most direct that could be discovered, and no special difficulties have been met.

4. Variation of Second Scions on Seedling Rootstocks.

Table I shows the variation of the second scions of Early Victoria in the percentage of shoots bearing terminal fruit buds.*

Since the number of "crowded" trees on Early Victoria intermediates is rather small, the figure for the larger number of trees next to a gap is also given.

Whilst "V" is lower for the trees on all the "stem-builder" intermediates than for those on Early Victoria, it is probable that, if the "crowded" trees

Table I.

Variation in percentage of shoots bearing terminal fruit buds: Early Victoria, end of 1935.

Intermediate.	Number of trees.	Coefficient of Variability "V" (From transformed data.)
Early Victoria "Crowded" ..	18	74·6
Early Victoria Next Gap ..	27	109·9
A "Crowded"	44	60·4
B ,, ...	40	61·3
C ,, ...	51	50·9

* Table I was kindly prepared for the writer by Mr. T. N. Hoblyn, who comments as follows:—

"In making a comparison of variability when the data are in the form of percentages, it is necessary to remember that normally the coefficient of variability will vary inversely with the size of the percentage. As, in the present instance, the trees on "stem-builder" intermediates all give higher percentages than those on Early Victoria intermediates, it is necessary to transform the data to a new scale which will be independent of this factor. In Table I the coefficients of variability are those obtained from the transformed percentages, use being made of the 'Inverse Size' transformation, a table of which is given by Fisher & Yates (1) and described also by Cochran (2)."

alone are taken, only the largest difference is significant. There is at least a strong probability that the very high variability in this character of the trees on seedling stocks has been reduced by the "stem-builder" intermediates; and it is unlikely that the reduction is merely associated with the greater size of the trees. It might well be that, as trees become more mature, their variability in this character also will be reduced. But in the present instance the trees were all of the same age; and since those on "stem-builder" intermediates were usually invigorated, their maturity is more likely to have been delayed than hastened.

Table II gives for both second scion varieties the percentage of trees above and below the average in size measurements in successive years. The only available records which can satisfactorily be used for this purpose are those here summarized.

TABLE II.

Percentage of trees on seedling stocks above *the average in one year, and* below *in the other. 1935 and 1936.*

Intermediate.	Early Victoria.		Newton Wonder.	
	Stem Increment (Area).	No. of Shoots.	Stem Increment (Area).	No. of Shoots.
Same as second scion ..	22·2	23·7	36·2	29·8
A	28·1	22·8	39·4	40·9
B	26·5	34·5	35·7	28·6
C	26·5	25·0	30·4	44·6

Whilst the differences are all small, and it is unlikely that any but the largest approach significance, those for Early Victoria are mainly in one direction; they are at least consistent with the possibility of some "evening up" influence of the "stem-builder" intermediates. Those for Newton Wonder are inconsistent, and except for "stem-builder" A could not be regarded as suggesting a tendency in the same direction.

It has been suggested that this result (with Early Victoria second scions) is merely another aspect of the reduced variation amongst the trees due to their greater size, already referred to. To the writer this seems unlikely, for the following reason.

The tendency of trees to "even up" as they become larger is probably due, at least in part, to the fact that large trees are closer than small trees of the same age to the upper limit in rate of growth. Where young trees are in nursery rows, this cause of "evening up" may be accentuated by root competition and perhaps by shading (though shading, when extreme enough to suppress the weaker individuals altogether, might have a contrary effect); and it will

probably have more effect the longer the trees remain in the nursery rows. Now, the groups expressed in Table II as percentages consisted actually of trees in two categories: those above the average in 1935 and below in 1936, and those below in 1935 and above in 1936. To the writer it seems to follow that the larger trees (i.e. those on "stem-builder" intermediates) should have a higher proportion than the smaller trees in the first of these categories, and a lower in the second. Actually, this was not so. With Early Victoria, where the "evening up" tendency was nearly consistent, the trees on "stem-builder" intermediates had a slightly larger proportion below the average in the first year and above in the second than those on Early Victoria intermediates.

5. THE COMPARATIVE INFLUENCE OF IX AND XII.

Here, unknown quantities are no longer being dealt with. The influence of these two vegetative apple stocks is not open to question; and it has been described (3) frequently enough to make it unnecessary here to go into details. Every scion variety so far tested has on IX made a very small quick cropping tree, and on XII a very large, very slow cropping tree. Some scion varieties may show the different influence of IX and XII to a more extreme extent than others; but none fails to show it very plainly. If "stem-builder" intermediates "even up" the performance of trees on variable seedling stocks, they should also, presumably, reduce this difference between trees on IX and XII.

The Influence of IX and XII on the Intermediates.

Measurements of the intermediates both before and after they were regrafted with the second scions, clearly show that all of them, "stem-builder" varieties as well as Early Victoria and Newton Wonder, were influenced similarly by IX and XII. The length of wood growth was in all cases greater on XII than on IX, in both the first and second year (before they were regrafted); the percentages by which the trees on XII exceeded those on IX for the two years together were as follows:—

Early Victoria 27, Newton Wonder 30, A 27, B and C each 32. There is little here to suggest that the "stem-builders" are less affected by rootstock influence than other varieties.

Table III, however, which summarizes the available stem size data for the intermediates, does suggest that there may be differences in this respect. The first measurement was made when the second scions were one year old; the figures given are those for "crowded" trees only.

The figures show by what percentages the stem sizes of the intermediates on XII were larger than those of the parallel intermediates on IX. Thus, at the end of 1934, the stem size of the Early Victoria intermediates on XII was 44% larger than that of the Early Victoria intermediates on IX.

The figures for the Early Victoria intermediates are with one exception higher than those for the comparable "stem-builder" intermediates; it seems probable that in stem size Early Victoria does show the difference between IX and XII to a somewhat greater extent than the "stem-builders". But the figures for the Newton Wonder intermediates are with one exception *lower* than those for the comparable "stem-builder" intermediates. Since in this case the second scions were all Newton Wonder, they were all pruned similarly; there has been no difference in treatment which could have contributed to the result.

It seems likely, then, that the stem size of Early Victoria is *more* affected, and of Newton Wonder *less* affected, by rootstock influence than that of the

TABLE III.

Stem size (area) of intermediates.

Figures for trees on XII given as per cent. of those for trees on IX.

"Crowded" trees only.

Intermediate.	Second Scion.					
	Early Victoria.			Newton Wonder.		
	End of 1934.	1935.	1936.	1934.	1935.	1936.
Same as Second Scion	144	194	244	116	127	147
A	150	191	231	149	148	170
B	129	157	194	129	134	143
C	130	172	214	144	151	165

three "stem-builder" varieties. Of the three "stem-builder" varieties, B is apparently less affected than A or C, and in much the same proportion with both second scion varieties. All these inferences are exactly confirmed by the figures for the trees next to gaps.

Since "stem-builder" intermediates do appear in Continental nurseries to produce good standard trees on seedling stocks, of which some would be too weak to produce such trees when single worked in the usual way, the intermediates must presumably invigorate the trees on the weaker stocks.

Table IV shows that, in the present trial, with one possible exception, they considerably invigorated the trees of both varieties on *all* stocks. If, therefore, they "even up" the trees on variable seedling stocks, it can be only by invigorating the trees on weak stocks proportionately more than those on vigorous stocks. Similarly, if the "stem-builder" intermediates reduce the difference in vigour between trees on IX and XII, it must be by increasing the vigour of those on IX proportionately more than that of those on XII. As regards vigour, this is what has to be looked for.

Since Table IV does not make this point easy to ascertain, the figures must be presented in a modified form. But Table IV brings out one point which requires much emphasis. Whether the "stem-builder" intermediates have reduced the difference between IX and XII or not, they are far indeed from having eliminated it. In vigour, a tree on IX still behaves as a tree on IX, and a tree on XII as a tree on XII, whatever the intermediate. The same point will be reiterated later, in regard to blossom and fruit bearing. Table IV

TABLE IV.

Effect of intermediates on vigour of second scion.

Conclusion of trial, April 1937.

Intermediate.	Second Scion. Early Victoria. Stem size sq. cm.	Early Victoria. Weight of Head. lb.	Newton Wonder. Stem size sq. cm.	Newton Wonder. Weight of Head. lb.
		On IX.		
Same as Second Scion	2·12	0·69	2·88	1·03
A	2·65	1·09	3·71	1·67
B	3·08	1·17	4·59	1·93
C	3·11	1·16	4·01	1·79
		On XII.		
Same as Second Scion	4·87	2·01	3·84	1·61
A	5·91	2·75	4·96	2·48
B	5·62	2·59	5·49	2·57
C	6·50	2·99	5·35	2·49
		On Seedling.		
Same as Second Scion	4·01	1·75	3·60	1·51
A	4·07	1·71	4·27	2·04
B	5·66	2·64	5·46	2·62
C	5·03	2·13	5·76	2·70

shows that, after only three years' growth, the stem size of Early Victoria on XII is twice that on IX ; whilst the weight of the head on XII is more nearly three times that on IX. In Newton Wonder the difference is smaller throughout ; it is quite probable that it was reduced by the severe pruning already referred to.

Table V gives all the available data for tree size in such a form that the differences between IX and XII can be seen at a glance. Here, as in Table III, the figures for the trees on XII are given as a percentage of those for the trees on IX. Thus, the maiden length of the second scions of Early Victoria on stems of Early Victoria on XII was 36% greater than that of the parallel second scions on IX ; whilst for the same series of trees, the weight of the head at the conclusion of the trial was 191% greater on XII—nearly three times as great.

The comparative effect of the intermediates is shown by a comparison of the figures in the same column. Thus, in the case just mentioned, whilst the weight of the head on XII was 191% greater than that on IX where the intermediate was Early Victoria, where it was B the difference was only 121%. Wherever the figures for A, B and C are lower than those for Early Victoria or Newton Wonder, the "stem-builder" intermediates *have* apparently reduced the difference between IX and XII.

The figures in the first and second columns show that, at the end of the first year's growth of the second scion, only one of the "stem-builders", B, gave any consistent indication of a tendency to reduce this difference. A year later, however, as shown both by actual stem size and by stem increment, all

TABLE V.

Tree size.

Figures for trees on XII given as per cent. of trees on IX.

Intermediate.	Maiden Length End of 1934.	Stem size (Area).			Stem increment (Area).		No. of Shoots.		Wt. of Head.
		End of 1934.	1935.	1936.	1935.	1936.	1935.	1936.	1936.
				Early Victoria.					
Early Victoria	136	115	186	229	244	281	143	175	291
A ..	154	138	176	223	211	297	145	181	252
B ..	134	128	151	182	174	230	107	155	221
C ..	148	138	174	209	207	258	133	149	258
				Newton Wonder.					
Newton Wonder	149	128	124	133	118	148	105	90	157
A ..	151	124	125	134	128	146	115	126	147
B ..	131	127	118	119	104	122	143	113	136
C ..	137	130	130	133	129	138	112	109	139

the "stem-builders" seem to have reduced the difference where the second scion was Early Victoria; and B also, where it was Newton Wonder. At the conclusion of the trial, a year later still, the same tendency is usually more marked in Newton Wonder, but slightly less marked in Early Victoria; it is most plainly shown by weight of head, where all the "stem-builders" had reduced the difference in both second scion varieties.

Of the three "stem-builder" varieties, B has almost consistently reduced the difference more than A or C, with both second scion varieties. The most notable exception is in the number of shoots of Newton Wonder produced in 1935. The figure given is that for the "crowded" trees; the few available trees next to a gap give a closely similar result. The writer is unable to suggest an explanation of this curious exception; it is the harder to account for, since other data collected from the same trees show no such tendency.

Had it been possible to continue the trial for a year or two longer, the results might have been considerably modified. Judging from the figures in Table V there is at least a possibility that, with Early Victoria, the maximum effect of the "stem-builder" intermediates in reducing the difference between IX and XII was obtained in 1935 ; the figures for both stem increment and number of shoots, which might be expected to reflect any change in behaviour more quickly than those for actual stem size, are somewhat closer together in 1936 than in 1935. In Newton Wonder the greatest reduction in the difference between IX and XII occurs in 1936 ; it is impossible to judge what might have happened subsequently. This difference in the behaviour of the two second scion varieties, again, may well be partly due to the difference in pruning treatment.

Significance of Results.

Since the trial was arranged in "balanced blocks" it has been possible to examine it statistically for soil variation in two directions. The result indicates that the trees to the east side of the plot were significantly larger than those to the west side ; whilst from north to south differences due to position were relatively slight and not significant. The fact that positional variation is significant in only one direction is encouraging. But as the plot measured 400 feet from north to south and only 24 feet from east to west, it may indicate merely that the extremes of soil variation occur in a relatively short distance. This is also suggested by a comparison of different units of the same treatment, where these occur close together. The very irregular distribution of the gaps, already referred to, makes it hardly worth while to analyse the records further.

The result as already presented, in figures calculated entirely from the records of "crowded" trees, is strikingly confirmed by those of trees next to a gap. This is true even of the greater effect of B than of A and C. But it would be possible to attach too much importance to this fact. The trees, it is true, are *different* trees ; the confirmation is of much more value than that obtained, for instance, from different measurements of the same trees. But the "crowded" trees and those next to a gap, in any one unit, occupied the same portion of row, and are therefore likely to be affected by soil variation in the same direction.

It may perhaps be concluded that, as far as vigour is concerned, there is clear evidence of some little influence of the "stem-builder" intermediates in the direction looked for. But, it must be repeated, rootstock influence still predominates ; at most only a slight "evening up" influence has been found, which could never come within a long distance of making trees on IX and XII behave similarly.

Blossom and Fruit.

Since the second scions were only three years old at the conclusion of the trial, it could hardly be expected that a very clear cut effect of the intermediates on precocity would be found. It is rather difficult, also, to judge what kind of effect, if any, might be expected. The fact that the "stem-builder" intermediates almost invariably invigorated the second scions, does not necessarily imply that they might be expected to reduce the amount of blossom they bore. Some of the records suggest that on any one stock the amount of blossom was roughly proportional to the size of the head. In any case, to give an intelligible result, amount of blossom must be in some way related to size of head; for various reasons none of the available records is for this purpose very satisfactory.

Table VI.

Number of fruit buds and fruits per tree; and fruits as a per cent. of fruit buds.

Intermediate.	Early Victoria.						Newton Wonder.		
	1935.			1936.			1936.		
	Buds.	Fruits.	Per cent.	Buds.	Fruits.	Per cent.	Buds.	Fruits.	Per cent.
					On IX.				
Same as Second Scion	18·3	11·2	61	5·9	11·9	200	6·1	1·2	19·3
A	21·4	8·8	41	22·9	19·5	85	4·9	0·6	12·1
B	25·8	9·4	36	16·3	22·1	136	8·8	1·2	12·5
C	22·5	8·8	39	15·7	23·1	147	8·9	1·1	11·2
					On XII.				
Same as Second Scion	0·4	0·1	25·0	6·0	2·3	38	0·0	—	—
A	0·8	0·0	—	9·3	4·5	48	0·0	—	—
B	2·9	0·5	17·2	3·7	4·0	110	0·0	—	—
C	1·2	0·2	16·7	3·8	2·7	72	0·0	—	—

Table VI summarizes the available records of both varieties, and gives also the percentage of the fruit *buds* represented by fruits (since each fruit bud produces several flowers, percentages above 100 are not unusual).

The figures for Newton Wonder can be disposed of briefly. The severe pruning of the trees at one year old may have delayed their cropping by as much as a year. None of the trees on XII produced any blossom; and few of those on seedling stocks produced more than an occasional fruit bud, in their last recorded year. (The trial was concluded too early in the winter of 1936-37 to allow of recording the fruit buds then present.) Even the trees on IX did not blossom appreciably until the same spring; a very few axillary fruit buds were, however, cut away in the pruning a year earlier.

Newton Wonder on two of the "stem-builder" intermediates on IX produced somewhat more fruit buds than the parallel trees on Newton Wonder

intermediates. Since the trees on the "stem-builders" were somewhat larger (Table IV), in these two cases the number of fruit buds may have been roughly proportional to tree size. On the third "stem-builder", A, the fruit buds were somewhat reduced in number. In the first year of cropping (1935) the second scions of Early Victoria, on both IX and XII, also produced slightly less fruit buds on A than on B and C; this, therefore, may not be due entirely to chance or local conditions. By itself, it cannot be regarded as of much importance.

Since the Newton Wonder trees on XII produced no fruit buds at all, it is impossible to judge whether, in precocity, the "stem-builder" intermediates reduced the difference between IX and XII. But it is abundantly clear that they did not obliterate the difference; in cropping, as in vigour, the trees on IX and XII behaved according to expectation, whatever the intermediate.

The trees of Early Victoria on IX blossomed to a considerable extent in 1935, and produced a moderate crop, in spite of the frost in May of that year (nearly all the blossom was axillary, and in consequence late opening; hence some of it escaped the frost). The trees on XII and seedling stocks produced a few fruit buds and a very few fruits, very irregularly distributed, as is usual on such trees. In 1936, a considerable number of the trees on IX had much less blossom (some few had none at all), than in 1935; they had already developed the biennial habit. At this time none of the trees on XII was biennial in any strict sense. A very few of them had less blossom than in 1935; but this was not the beginning of the biennial habit, as is shown by the fact that those of any treatment which had more than the mean number of fruit buds in 1935, as a group, in the majority of cases again had more than the mean number in 1936. This could not occur if the trees were really biennial.

Table VI shows that the biennial habit of the trees on IX was much more extreme, as measured by fruit buds, where the intermediate was Early Victoria than where it was A, B or C. On Early Victoria intermediates the mean number of fruit buds was reduced to less than one third, whilst on A, B and C it was reduced comparatively little or not at all. The difference is best shown by the "biennial intensity", calculated by Hoblyn's method (4). Those trees on Early Victoria intermediates which had less fruit buds in 1936 than in 1935, amounting to 81% of the whole, had an intensity of 0·82; for A the corresponding figures are 74% and 0·60; for B, 75% and 0·55; and for C, 83% and 0·51.

This difference in the intensity of the biennial habit makes it exceedingly difficult to discover whether, or to what extent, the "stem-builder" intermediates have reduced the difference in precocity of the trees on IX and XII. It becomes almost impossible to use for this purpose the figures for 1936; only those for 1935 can be used, and here so many of the trees on XII had no blossom at all that any calculations based on them are liable to be misleading.

The figures do, however, suggest that the "stem-builder" intermediates may have reduced the difference considerably. On IX the trees on "stem-builders" had only slightly more blossom than on Early Victoria intermediates; whilst on XII the trees on Early Victoria intermediates were proportionately very much farther behind. But where the average is less than 1 per tree, a very small difference in the numbers recorded would make a very large difference in the result. It is not therefore possible to regard this result as more than an indication.

The differences in blossom setting are wide, and, on IX, consistent. Both varieties on IX set their blossom much better where the intermediate was of the same variety as the head, than where it was a "stem-builder". On XII, only the figures for 1936 can carry any weight; those for 1935 are too low. In 1936, the result is the reverse of that of the trees on IX, the set on Early Victoria intermediates being lowest instead of highest. Now, it has become a commonplace that blossom setting is closely correlated with vigour; and there is probably, for any particular conditions, an "optimum" vigour for setting. But in this instance the best set is found on the *least* vigorous trees on the dwarfing stock, IX, and on the *most* vigorous trees on the very vigorous stock, XII, precisely the reverse of what might have been expected.

As far as the Early Victoria trees on IX are concerned, the heavy set in 1936 of those on Early Victoria intermediates is doubtless connected with their high biennial intensity, and the resulting small amount of their blossom. It has been commonly observed that strongly "off year" trees of Early Victoria tend to set a very high proportion of the few blossoms they produce. But this explanation cannot apply to the remaining instances; and the behaviour of the trees on XII, in particular, seems at present quite inexplicable. Of the known factors controlling blossom set, none seems to have any bearing on this instance.

6. Stem Size of Trees.

The Continental claim that trees raised by the "stem-builder" process have stouter stems than similar low worked trees is fully borne out by the trial. With Early Victoria, the "stem-builder" intermediates were stouter on all stocks than those of Early Victoria, by an amount ranging from 4 to 41%; the differences were proportionately greater on IX than on XII and seedling stocks.

The "stem-builder" stems were also stouter than those of Newton Wonder on XII and seedling stocks; but on IX those of A and C were very slightly more slender than those of Newton Wonder. It is noticeable that on IX, with both second scion varieties, B made considerably stouter stems than A or C; whilst on XII and seedling stocks the difference was smaller and was sometimes reversed.

7. Proportion of Good Standard Trees.

Since the trees in the present trial, with the exception already noted, were allowed to form their heads without pruning, it is not possible to judge exactly what proportion would have made saleable standards. It is possible, however, to use instead the percentage of intermediates which were not tall enough at two years old to be regrafted. These data are summarized in Table VII.

Table VII.

Percentage of intermediates not tall enough to rework at two years old.

Intermediate.	IX.	XII.	Seedling.
Early Victoria	16·4	1·9	0·0
Newton Wonder	9·7	0·0	1·6
A	1·6	0·0	1·5
B	2·8	0·0	4·1
C	4·4	0·0	0·0

It is plain that the "stem-builder" process would have somewhat reduced the proportion of failures on IX, particularly of Early Victoria. (Percentages below 2 represent only one or two trees each, and can be disregarded.) The figures do not, of course, adequately represent the difference in commercial value of the groups of trees. The fact that the heads formed by the second scions were larger on "stem-builder" intermediates has already been shown (Table IV). The third claim for the "stem-builder" process can therefore be accepted as justified.

8. Discussion.

It appears, then, that the claims of Continental nurserymen for the "stem-builder" process can all be accepted, up to a point. "Stem-builder" intermediates, at least of the three varieties used in the trial (many others have been used on the Continent), do produce trees with stouter stems; they do produce a larger proportion of good trees in the nursery; and they also tend to even up the different influences on vigour of different rootstocks. But their effect in this last direction has in the present trial been comparatively slight; with the two vegetative stocks it was far outweighed by rootstock influence. It does not at present seem probable that any but comparatively slight rootstock influences could be completely eliminated by the use of any of the three "stem-builder" varieties tested.

As far as rootstock influence on vigour is concerned, any apparent "evening up" may perhaps be accounted for, as has been suggested, by the invigorating effect of the "stem-builder" intermediates on the second scions. The suggestion is that any such invigoration would be likely to be proportionately greater

amongst the weak trees than amongst the vigorous trees, for the reason that the latter are closer to the upper limit of rate of growth than are the former. But it seems unlikely that invigoration alone will account for the "evening up" of rootstock influence on the relationship between growth and blossom formation, shown in Table I. It is worth noting also that "stem-builder" B, which "evened up" rootstock influence on vigour more than A or C (Table V), appears in Table I to have had *less* influence than either A or C.

There is at least a possibility that other varieties, not yet tested as "stem-builders" at East Malling, might give still more effect in the same directions. But the prospect of ever obtaining a similar performance from trees on rootstocks of widely different influence, by the use of any one intermediate variety, seems remote. Since other investigations on double working at East Malling have revealed intermediates of widely different influence, some dwarfing and some invigorating, it might be possible by using *different* intermediates to make the performances of trees on IX and XII approach much more closely than they did in the present trial. But such a method could be applied only where rootstock influence is already known; it could not be used with unknown seedling stocks.

The permanent or temporary nature of the "stem-builder" influence could not have been proved without a much longer continued trial. The only evidence secured is, however, suggestive; the quickly maturing variety, Early Victoria, when used as second scion, showed no increase in the "stem-builder" influence after the second year, but rather a falling off. On this question nothing further can as yet be said; only a long time trial of such trees in orchard as well as nursery could solve it.

In conclusion, the writer would like to express his personal thanks to many members, past and present, of the East Malling staff, particularly of the Pomology and Propagation Sections; and to the Statistics Section for an analysis of part of the records and much help in examining the remainder.

SUMMARY.

A report is given of a trial of certain apple varieties used in Continental nurseries as "stem-builders"; it is claimed on the Continent that standard trees on seedling stocks, double worked on stems of these varieties, give three advantages: stouter stems; a larger proportion of saleable trees; and larger heads. These claims are found to be at least partially justified.

The claim that a larger proportion of good trees is obtained implies a reduction of rootstock influence on vigour; this is examined in detail by means of trees on seedling rootstocks and also by a comparison of trees on a dwarfing and a vigorous vegetative stock. Of the two second scion varieties used for

the purpose, one, Early Victoria, appears to show the reduction of rootstock influence by the "stem-builder" intermediates plainly; the other, Newton Wonder, gives an indefinite result.

The "stem-builder" intermediates may have influenced both the development of the biennial habit amongst the trees of Early Victoria on the dwarfing rootstock, IX, and the set of fruit of both varieties on IX, and of Early Victoria also on XII.

REFERENCES.

(1) *Fisher, R. A.* and *Yates, F.* Statistical Tables for Biological, Agricultural and Medical Research. Oliver & Boyd, 1938, p. 42.

(2) *Cochran, W. G.* Some Difficulties in the Statistical Analysis of Replicated Experiments. Empire Journ. of Expt. Agri., 1938, **6**, 22.

(3) *Hatton, R. G.* Apple Rootstock Studies. Effect of Layered Stocks upon the Vigour and Cropping of Certain Scions. Journ. Pom. & Hort. Sci., 1935, **13**, 293.

(4) *Hoblyn, T. N. and others.* Studies in Biennial Bearing, I. Journ. Pom. & Hort. Sci., 1936, **14**, 39.

(*Received* 22/12/38.)

THE INFLUENCE OF "STEM-BUILDER" INTERMEDIATES ON APPLE ROOT SYSTEMS

By W. S. ROGERS, A. BERYL BEAKBANE and CAROL P. FIELD
East Malling Research Station

THE root systems of the series of double-worked apple trees described in the foregoing paper by Grubb (1) were studied in February 1937. The trees were worked on two vegetatively propagated rootstocks, Nos. IX and XII, and on a collection of seedlings obtained from a trade source. The rootstocks were budded in 1932, at three inches above ground level, with three "stem-builder" intermediates obtained from a nursery in South Germany and with the two varieties chosen for second scions as control. The "stem-builders" were Noir de Vitry, Normanischer Ciderapfel and Gelber Trier'scher Weinapfel, referred to as A, B and C respectively in the following pages. The intermediates were "run-up" and re-worked at five feet above the first union with Early Victoria and Newton Wonder as second scion varieties. Three separate studies were made as described below.

I. EXCAVATION OF COMPLETE ROOT SYSTEMS.

The entire root systems of twenty-four four-year-old Early Victoria trees were excavated in detail by the "skeleton" method described by Rogers and Vyvyan (2). The trees were on two vegetatively propagated rootstocks worked with two intermediates as shown below.

Rootstock.	First Scion (Intermediate).	Second Scion.
IX	Early Victoria	Early Victoria
IX	Normanischer Ciderapfel (B)	Early Victoria
XII	Early Victoria	Early Victoria
XII	Normanischer Ciderapfel (B)	Early Victoria

SOIL.

The soil in which the trees were growing is the Malling series of the Lower Greensand with a top soil of medium loam about 25 cm. in depth and a sandier subsoil overlying a heavy sticky layer known as "pug" which varied in thickness from 5 to 28 cm. Beneath the "pug" was a loose uncemented rock

material called "hassock" which overlies the ragstone rock in most places. The depth of the "hassock" varied from 80 to 150 cm. below ground level where the trees with Early Victoria as intermediate were excavated, and from 105 to 150 cm. beneath the trees with intermediate B. In this position it was also noted that a layer of sand and gravel occurred in a few spots at a depth of from 50 to 70 cm.

Root Distribution.

The roots from neighbouring trees were found to be very closely intermingled under these conditions of close planting in nursery rows at 15 inches by 4 feet. Alternate trees were, therefore, injected with a dye ("light green") before excavation, so that the roots of the individual trees might be identified with greater accuracy. Even so, the tracing of the roots of each tree was a complicated matter, as can be seen from the root plans, Fig. 5, and from the photographs of the re-arranged root systems, Figs. 1 to 4. Fig. 5 also shows the marked restriction of root growth in the direction in which root competition was greatest. The root plans of the trees on XII (not reproduced) showed a larger root spread and even more intense root competition.

In all cases the deepest roots went down to the "hassock" or the rock, and the general depth of root did not appear to be influenced by the "stem-builder".

Effect of "Stem-builder" Intermediates.

The records of the above ground parts of the trees reported by Grubb (1) show that the "stem-builders" considerably invigorated the trees of both varieties on all rootstocks, but that the increase in vigour of trees on IX was proportionally more than that of those on XII. This invigorating effect was clearly visible in the root systems of the excavated trees on IX and is shown in Figs. 1 and 2 and in the root plans, Fig. 5. The roots of the trees on IX with intermediate B weighed 60% more than those with Early Victoria as intermediate. No marked contrast was visible between the two sets of trees on XII, however, and, in the samples excavated, some were actually rather smaller with intermediate B than with Early Victoria as intermediate (see Figs. 3 and 4). This is probably due to the fact that, in the randomized planning of the plot, this particular line of trees with Early Victoria intermediate had weaker trees on each side of it than the line of trees with intermediate B, and that the difference in root competition has masked the small increase in the vigour of XII which might have been expected with intermediate B.

It is evident that the "stem-builder" by no means eliminated, although it reduced, the difference in size between the root systems of IX and XII. Further, it did not appear to have any considerable qualitative effect on the root systems, which remained typical of IX and XII in appearance, whether

Fig. 5.

Root Plans of sections of nursery rows of Early Victoria on No. IX rootstock with intermediates of (1) Early Victoria, and (2) Normanischer Ciderapfel. Note the greater vigour of (2) and the directional effect of the intense root competition. The roots of alternate trees are shown with dotted lines to make them more easily distinguishable.

worked with Early Victoria or with B as intermediate. This is clearly shown in Figs. 1 to 4. The IX root systems worked with both intermediates showed the characteristic brittle nature of the roots and had a number of fine roots near the main stem in contrast to the tougher and coarser roots of XII.

II. OBSERVATIONS ON MAIN ROOTS OF ALL SERIES OF TREES.

The main part of the root systems of the whole series described by Grubb, including trees of both Newton Wonder and Early Victoria, each re-worked on the same variety and on the "stem-builders" A, B and C on rootstocks IX, XII and on a collection of seedlings, were carefully lifted with a circle of roots surrounding the stock stem to a distance of about 18 inches. Four hundred and eighty trees, including twenty-four combinations of rootstock, intermediate and second scion, were examined for collar fibre (small roots arising from the stock stem), coarseness, straightness and direction (position tending to be vertical or horizontal). The IX root systems were found to have more collar fibre than those of XII or of most of the seedlings. The roots of a number of the seedlings followed a markedly sinuous course in contrast to the straighter roots of IX and XII. The roots of XII were found to be rather straighter and far coarser than those of IX and were even coarser than those of most of the seedlings. Many of the seedlings had roots which descended more nearly vertical from the base of the stock stem than those of IX or XII. None of these characteristics appeared to be markedly influenced by any of the "stem-builders" (see Fig. 6).

The seedlings showed a far greater range of variation among themselves, in the four characteristics listed above, than the trees on IX or on XII. The variation between specimen seedling rootstocks worked in the same way is well shown in Fig. 6.

III. STEM:ROOT RATIOS.

When the main series of trees was lifted, the trees were sawn off at the union between the rootstock and the intermediate, i.e. at about ground level. The weight of the stem above the top of the rootstock and the weight of the central part of the root system was obtained on 480 trees. The figures were used to give a rough index of the stem:root ratio (see Table I). It should be noted, however, that these figures are not comparable with the ratios given in other studies (2), since, in the present case, the "root weight" actually consists of the weight of the stock stem and the roots to a length of only 12 inches. Where the weight of the whole root system was obtained, as in Study I, it was found that the ratio of the stem weight to roots plus stock stem was about half that given in Table I for similar stock:scion combinations, i.e. the weight of

TABLE I.

Second Scion.	Rootstock.	"Root weight" lb. per tree.						Stem : Root Ratio.					
		Intermediate.						Intermediate.					
		A	B	C	E. Vic.	Newton.	Mean.	A	B	C	E. Vic.	Newton.	Mean.
Early Victoria.	IX	1·1	1·1	1·1	1·0	—	**1·1**	2·5	2·8	2·6	2·5	—	**2·6**
	XII	2·3	2·1	2·2	2·1	—	**2·2**	3·2	2·9	2·8	2·1	—	**2·8**
	S	2·3	2·8	2·8	2·2	—	**2·5**	2·1	2·2	1·9	2·1	—	**2·1**
	Mean	**1·9**	**2·0**	**2·0**	**1·8**	—	**1·9**	**2·6**	**2·6**	**2·4**	**2·2**	—	**2·5**
Newton Wonder.	IX	1·0	1·1	0·9	—	0·8	**0·9**	3·3	3·5	3·2	—	3·7	**3·4**
	XII	1·4	1·4	1·7	—	1·2	**1·4**	3·8	3·0	2·8	—	3·3	**3·2**
	S	1·9	1·9	1·8	—	1·5	**1·7**	2·5	2·6	2·6	—	2·4	**2·5**
	Mean	**1·4**	**1·5**	**1·5**	—	**1·2**	**1·4**	**3·2**	**3·0**	**2·9**	—	**3·1**	**3·0**

the stock stem and roots to a length of 12 inches was about equal to the weight of the rest of the root system, which was not obtained in Study III. The proportion of the "root weight" that consisted of stock stem varied, however, from about 55% in small trees to 35% in large trees. It cannot be said, therefore, that these "root weight" figures bear an exact and constant relationship to the total weight of the complete root system. Nevertheless, these ratios are of interest as giving a rough comparison between the above and below ground portions of the tree. The greatest differences in the weights of the central parts of the root systems were found to be between the trees on different rootstocks (see Table I). The average "root weight" for all the Early Victoria trees on IX is 1·1; on XII, 2·2; on seedlings, 2·5 lb. The difference in "root weight" between trees worked with different intermediates is not nearly so great as that between trees on different rootstocks. There is a considerable difference between the two varieties, however; for trees with Early Victoria as second scion the average weight is 1·9, while for Newton Wonder it is only 1·4 lb. Both the root and stem weights were less in trees with Newton Wonder than with Early Victoria as second scion. The ratio of stem weight to root weight, however, was higher with Newton Wonder than with Early Victoria, the former being 3·0 and the latter 2·4, i.e. the Newton Wonder trees had a heavier stem system per unit weight of root than the Early Victoria trees (see Table I). The lowest stem:root ratio was 2·1 for trees of Early Victoria on seedlings and the highest was 3·4 for Newton Wonder on IX. The stem:root ratios of the trees worked with different intermediates are very similar, as shown in Table I.

Trees which were next to gaps are excluded from Table I, since it was found that the lessened competition increased their vigour. The stem:root ratios for trees next to one gap were calculated separately, however, and were found to be practically similar to those given in Table I.

SUMMARY.

1. The conformation and relative size of the root systems of twenty-four double-worked apple trees, excavated in detail, are illustrated and discussed. The trees were Early Victoria on rootstocks Nos. IX and XII with 5 ft. intermediate stem-pieces of Normanischer Ciderapfel and Early Victoria. The introduction of the "stem-builder" intermediate, Normanischer Ciderapfel, was found to have reduced the difference in size due to rootstock by invigorating the trees on No. IX. The morphological characteristics of the rootstocks were not influenced by the "stem-builder" intermediate.

2. Observations on the main roots of 480 double-worked apple trees are presented. The series comprised Early Victoria and Newton Wonder each re-worked on 5 ft. intermediate stems of the same variety and on Noir de Vitry,

Normanischer Ciderapfel and Gelber Trier'scher Weinapfel, on rootstocks No. IX, No. XII and a collection of seedlings. None of the intermediates materially altered the morphological characteristics of the rootstocks Nos. IX and XII, nor did they eliminate variations among the seedling rootstocks.

3. " Root weights " consisting of the central part of the root system with the stock stem attached, were obtained for the 480 trees described above. The results are tabulated and stem : root ratios presented. The " root weights " showed that the difference in vigour of the root systems normally found between the dwarfing No. IX and the vigorous No. XII was not eliminated, though it was somewhat modified, by the introduction of the long " stem-builder " intermediates. Trees of Newton Wonder were found to have a higher stem : root ratio than those of Early Victoria. Little difference in stem : root ratio was found between trees worked with different intermediates.

REFERENCES.

(1) *Grubb, N. H.* The Influence of the Intermediate in Double Worked Apple Trees: Nursery Trials of the " Stem-Builder " Process at East Malling. Journ. Pom. & Hort. Sci., 1939, **17**, 1.

(2) *Rogers, W. S.* and *Vyvyan, M. C.* The Root Systems of Some Ten-Year-Old Apple Trees on Two Different Rootstocks, and their Relation to Tree Performance. East Malling Res. Sta. Ann. Rept. for 1926-27 (II Supplement), 1928, 31.

(*Received* 25/11/38.)

FIG. 1.

Early Victoria on No. IX rootstock with a 5 ft. intermediate stem-piece of Early Victoria.

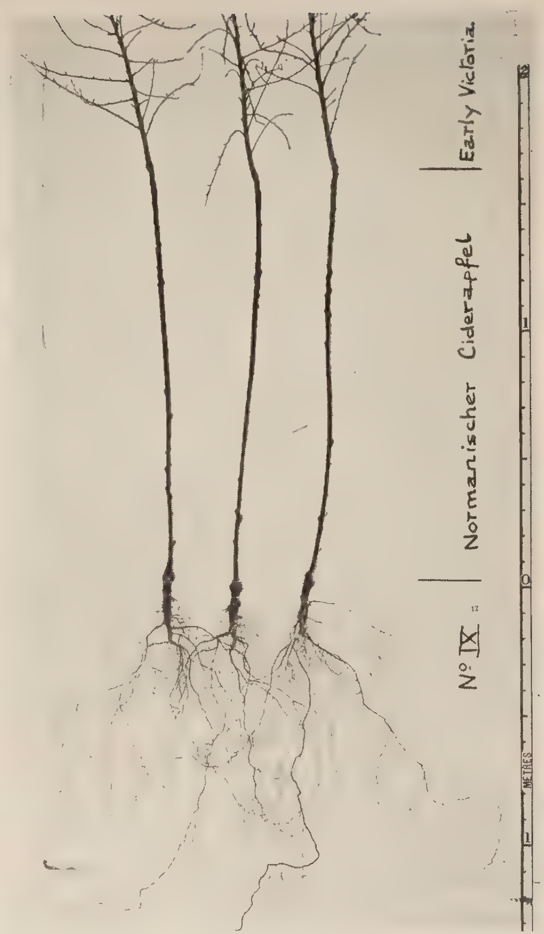


FIG. 2.

Early Victoria on No. IX rootstock with a 5 ft. intermediate stem-piece of Normanischer Ciderapfel. Note that the vigour of both stems and roots is greater than in Fig. 1.

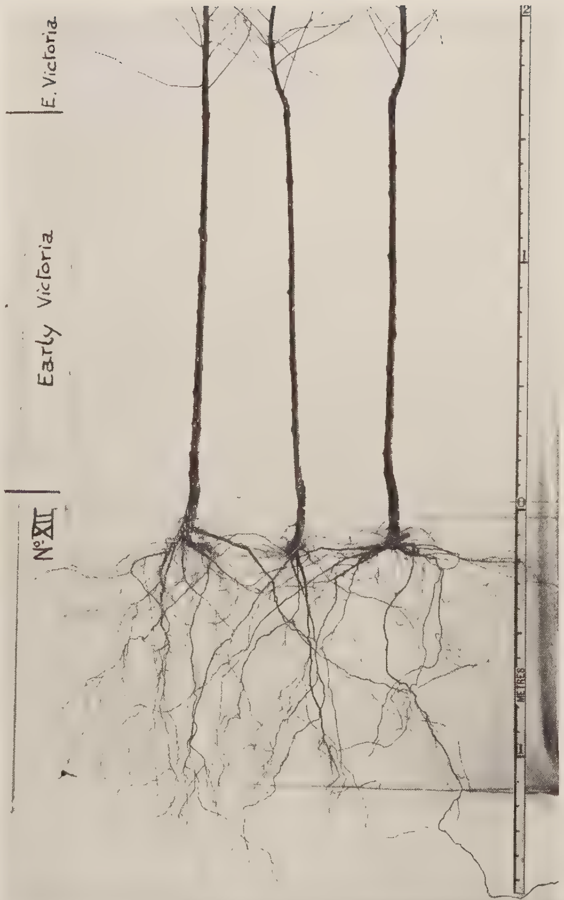


Fig. 3.

Early Victoria on No. XII rootstock with a 5 ft. intermediate stem-piece of Early Victoria. Note the contrast between the No. XII root system and the No. IX shown in Fig. 1.

Fig. 4.

Early Victoria on No. XII rootstock with a 5 ft. intermediate stem-piece of Normanischer Ciderapfel. Note the absence of marked contrast in vigour with Fig. 3 and the severe root competition.

FIG. 6.

Specimen seedling rootstocks which were worked with intermediate stem-pieces of Newton Wonder (left), Normanischer Ciderapfel (centre), and Gelber Trier'scher Weinapfel (right) all with Newton Wonder as second scion. Note that within each series large variations in vigour and root characteristics remain visible.

ON THE OCCURRENCE AND SPREAD OF THE RING SPOT DISEASE OF LETTUCE CAUSED BY *MARSSONINA PANATTONIANA* (BERL.) MAGN.

By GRETA B. STEVENSON
Imperial College of Science and Technology, South Kensington

I. INTRODUCTION.

LETTUCE is one of the more difficult crops to raise satisfactorily for the market because it is the foliage, the part most readily injured, which is required to be free from blemish. The fungus, *Marssonina Panattoniana,* in epidemic form, rapidly destroys lettuce seedlings and may also bring about the death of older plants, but even a mild attack causes such unsightly browning and perforation of the leaves as to render the heads unsaleable. A degree of attack, therefore, which may be of no consequence in another crop, may be very serious to the lettuce grower.

Ring Spot, the common name* accepted in this country for the disease caused by the fungus mentioned, has been widespread in temperate regions from an early date, having been reported from Italy by Berlese (2) in 1895 and at almost the same time from America by Selby (15). Berlese named the causal organism *Marssonia Panattoniana* and Selby, independently, called it *Marssonia perforans*. Within the succeeding twenty years the disease was noted in many other countries, where attention was drawn to it by the destructive nature of the outbreaks. In the Netherlands, for example, it was recorded in 1899 (Oudemans (11)) and in Michigan in 1906 by Dandeno (6). The latter author renamed the fungus *Didymaria perforans* but Magnus (8), examining its synonymy, gave priority to Berlese's specific name. It was necessary to alter the generic name from Marssonia to Marssonina because there was already a phanerogamic genus of the first name ; thus the name of the fungus became established as *Marssonina Panattoniana* (Berl.) Magn.

In 1907 an epidemic was recorded by Appel and Laibach (1) in Germany, causing considerable losses of lettuce in the field. In England it was first noticed in 1912 (Chittenden (5)) and two years later an account was given by Marchal and Foëx (9) of its occurrence in France. In 1919 it was reported from Australia (Birmingham (3)). Appel and Laibach, who considered that

* By growers the disease is sometimes called Rust, a misleading term and one to be avoided. In America and elsewhere it is called Anthracnose. (See the British Mycological Society's List of Common Names of British Plant Diseases. Cambridge University Press, 2nd edition, 1934.)

the disease had been present in Germany for some years, found that it was prevalent in cold wet weather. They examined the fungus in culture and carried out inoculation experiments, showing that penetration was through the epidermis but between the epidermal cells. Groups of short conidiophores, bearing spores singly, broke through the epidermis forming a whitish centre to the leaf lesion. At a later stage the centre of the lesion dropped out and a ring of spores surrounded a small hole. Appel and Laibach suggested that the fungus was probably related to *Ascochyta Lactucae.*

Destructive outbreaks of the disease in greenhouse crops of "leaf" lettuce* in America led to an investigation by Brandes (4) who isolated the fungus and carried out inoculation experiments showing that the disease occurred only under cold, wet conditions, an observation which agreed with that of Appel and Laibach. Brandes concluded that once infection had occurred the fungus was able to spread in the host tissue under ordinary greenhouse conditions as easily as in a specially humid atmosphere and that therefore, apart from the relation of water to spore dissemination and germination, temperature played a more important part in infection than moisture. He found that the fungus had an optimum temperature for growth in culture of 20° C. Chlamydospores were formed in cultures on various media. The conidia, which would not withstand more than five days' desiccation on coverslips, did not germinate above 28° C., and had a thermal death point of 40° C. They germinated readily in 4 to 8 hours at 25° C. and young colonies 30 to 40 hours old were already producing new conidia. On the surface of a lettuce leaf germination was equally quick, penetration through the epidermis being observed and the hyphae always remaining intercellular.

Brandes suggested that as the disease appeared suddenly in the U.S.A. on ground which had not previously borne a lettuce crop it might be seed-borne, and further, that as the symptoms appeared first on the outer leaves and spread to the inner ones, infection probably took place from the soil. He showed that diseased leaves buried in sand for a period of two and a half months contained viable spores. The control measures advised were to eliminate overhead watering in the houses, to give good ventilation so as to keep the leaves as dry as possible and, if necessary, to raise the temperature.

All the varieties of lettuce (*Lactuca sativa*) with which Brandes experimented proved to be highly susceptible, but all attempts to inoculate the related species *L. floridana, L. Scariola* and *Cichorium Intybus* failed. At a later date some further experimental work was done in America on this aspect of the problem by Parker (13) who isolated *M. Panattoniana* from diseased lettuce and inoculated *L. Scariola* with the isolate, thereby obtaining perfect infection. This plant,

* By "leaf" lettuce is understood young immature plants gathered for salad in mass, as opposed to older, "hearted", individual plants gathered as such.

growing in the open as a weed, was also found to be infected naturally with the same fungus.

In 1922 a serious outbreak of the disease occurred at Swanley in Kent, and an investigation was made by Salmon and Wormald (14) who gave a possible explanation for the epidemic in the use of manure which may have contained market refuse, including lettuce trash, from infected continental areas. For control measures they suggested spraying with a fungicide and adopting a system of rotation, as the disease is usually continued from the remains of a preceding diseased crop.

In Hungary in 1928 (Kern (7)) *M. Panattoniana* was so virulent on lettuce as to threaten destruction of the seed-bearing plants. Pape (12) found it on lettuce seed-bearers in Germany but stated that the spores were not carried on the seed and that it was uncertain whether the fungus persisted in any of the plant organs as resting mycelium.

Recent records of the Ring Spot disease in England include that of Ogilvie (10) who made observations in the field as to the varieties showing the greatest attack. Wortley (18), investigating the effect of lithium salts on resistance to disease, found that the application of a 1% solution of lithium nitrate reduced the amount of Ring Spot without adversely affecting the plants.

The disease has been under observation at the Biological Field Station of the Imperial College of Science and Technology at Slough, from the year 1931 onwards. The general result of preliminary work was to confirm the conclusions of earlier workers that the disease is favoured by wet, cold weather in spring and early summer. The further work to be described in the present paper relates chiefly to investigations during the period 1935-38.

II. SYMPTOMS.

The appearance of diseased plants has been described and figured by Appel and Laibach, by Brandes, and by Salmon and Wormald, but it is worthy of further discussion, as certain other diseases may produce closely similar injury. The most characteristic symptom of Ring Spot, in the writer's experience, is the development of small round holes, about 2 mm. in diameter, on the green parts of the lettuce leaf. Occasionally the holes may run together and thus become irregular and simulate animal injury, but usually the typical small round holes are also present. Under favourable conditions such perforations may have a pale pink fringe of spore masses, but most commonly the edges of the holes are brown.

On the stem, or on the veins of the leaves, the fungus produces irregular, sunken, brown lesions, usually approximately oval in outline which are so closely similar to various forms of slug attack and to the symptoms of some

bacterial diseases that they can be identified for certain as being caused by Marssonina only if the fungus is isolated from them or if they are found in association with small round holes in the leaves. Similar lesions, probably due to *Rhizoctonia Solani,* are found commonly on the stems of lettuce seedlings.

The earlier stages of the disease are not so easily distinguished. Usually infection begins in the form of small brown spots on the lamina and these may extend to about 2 mm. in diameter before Marssonina spores are seen on them or the centre drops out to form the typical "shot" holes. Leaf spots which to the naked eye appear almost identical with these may be caused by various bacterial pathogens of lettuce, and occasionally by *Botrytis cinerea*. Leaf spotting by the latter fungus was produced artificially by spraying seedlings with spores of a strain isolated from lettuce. Identical spotting was frequently seen on the cotyledons of seedlings in frames, especially where the seed coat had hung on the tip of the seed leaf, thus forming a damp chamber. *B. cinerea* lesions tend to dry up and form small black spots, in which form they are easily distinguished from those due to *M. Panattoniana* which remain brown. Leaf spots due to bacteria tend to be more of a yellow-brown colour than those caused by Marssonina.

Under cold, wet conditions, favourable for the rapid development of the disease, especially on young seedlings, the fungus frequently does not remain in a restricted spot but spreads rapidly over irregular areas 1 cm. or more across, which are watersoaked and rapidly become browned and destroyed. In such cases the rotted leaf becomes a brown, slimy mass on which the fungus produces spores much less freely than on the restricted leaf spots.

The fungus, when present, is readily demonstrated by keeping the material for two or three days in a damp chamber, when masses of spores are produced. This test has always been used by the writer as the criterion whenever there was any doubt as to the cause of disease.

III. METHODS OF LETTUCE CULTIVATION AND THE OCCURRENCE OF RING SPOT ON COMMERCIAL CROPS.

In England "head" (i.e. hearted) lettuce is raised under glass during the months November to March. The writer has not seen Ring Spot on this type of crop and, although the disease has once been reported under such conditions in this country (Chittenden (5)), it has not been noted since and is commercially of no importance. Glasshouse crops of "leaf" lettuce, such as Brandes described and as are also grown in France, are not raised in England. Lettuce is grown under glass in frames on hot beds or semi-hot beds in February, March and April, but there also the crop is in practice free from the disease.

Lettuce raised by either of the above methods is expensive and supplies a limited luxury market. The great bulk of the salad crop consumed in England is matured in the open, and three classes of culture may be distinguished:—

1. *Summer lettuce,* the seed of which is drilled in the field from spring to the middle of summer to give a continuous supply from summer to autumn. As this crop is produced under weather conditions normally unfavourable to Ring Spot, the disease is of little commercial importance in this connection. Growers report having seen the disease in certain years during the summer, but this has not occurred in the writer's experience. If a late crop is grown, to mature in October-November, and these months are wet, the plants are often slightly infected.

2. *Spring lettuce,* which is derived from seedlings planted out in the field from frames in the early spring to supply the market before the summer lettuce crop is ready. The seed of this is sown broadcast in cold frames or, on a smaller scale, the young plants are pricked out in the autumn to stand the winter under glass lights. Ring Spot is of very rare occurrence in the frames, for it can develop in them only when they are allowed to become wetter than is good practice. The disease may appear on the plants in the field later, even though they were apparently free from it at the time of transplanting. This occurrence was noticed in one garden where planting was done very early in the wet spring of 1937. The longer spring lettuce is exposed to cool, wet weather, i.e. the earlier it is planted out, the more chance there is of its developing the disease ; but on the whole spring lettuce is not much troubled with Ring Spot.

3. *Winter lettuce,* the crop on which this disease is of greatest importance, is produced from seed sown in August or September—either broadcast or in drills—and the plants stand in the open throughout the winter to head up in the late spring and early summer before the spring lettuce crop matures. Transplanting may be carried out in October or November, or it may be postponed until January, February or March. Alternatively, the seed is drilled in the open field to stand the winter there in the seedling stage and is thinned or "struck out" in the spring.

As this crop is early on the market it commands a good price, and as it is also less expensive to grow than spring lettuce, which requires much attention while in the frames, it is extensively grown in the market gardening area supplying London and other large towns in the South of England. It is often said that winter lettuce is tough, and there is therefore a certain amount of prejudice against it. With both spring and winter lettuce, the part which is sold has developed over approximately the same period of the year and under the same conditions, so that, apart from possible differences in the varieties

used, it is difficult to see what basis there could be for a difference in quality. It may be suggested that the prejudice is based on the fact that winter lettuce is often more or less blemished by Ring Spot attack whereas spring lettuce normally is free from it.

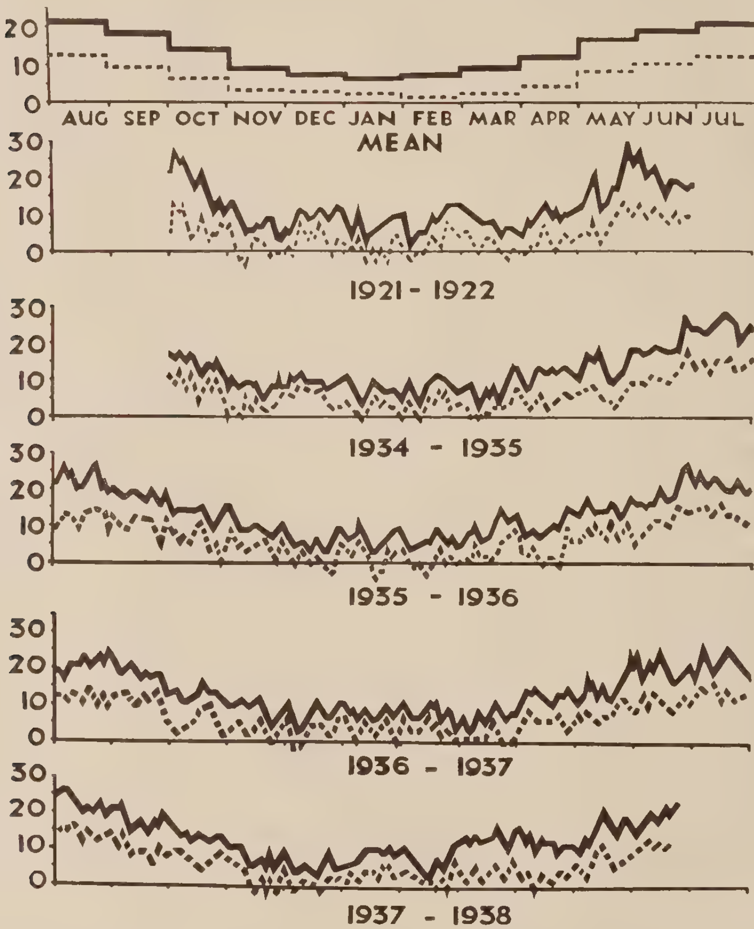


Fig. 1.

Maximum and minimum temperatures (° C.) at Kew, in 1921-22 and 1934-38.

Text-figures 1 and 2 give the records of temperature and rainfall throughout the growing period for winter lettuce for the past four seasons and also for 1921-22, when the disease was very serious in Kent. It is seen that the spring of 1922 was almost continuously very wet and at the same time fairly mild. These conditions are known to be suitable for large-scale development

of the disease. In the seasons 1934-35 and 1935-36 the disease was prominent at the Biological Field Station, Slough, and at the few commercial places which were visited. Extensive field observations were made during 1936-37 and

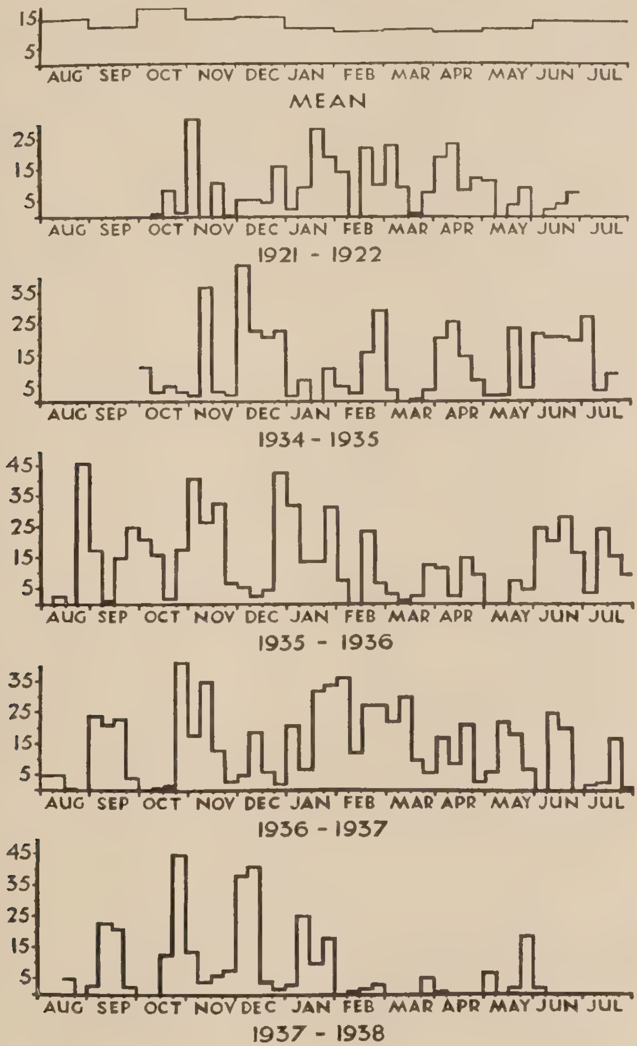


FIG. 2.

Rainfall (mm.) per quarter-month at Kew, in 1921-22 and 1934-38.

1937-38 which were, as shown by Figs. 1 and 2, exceptional years. The former winter was unusually wet, especially during the months January to March, whereas the latter was extremely dry from February onwards. In accordance

with this, the disease was rampant in the spring of 1937 but almost absent in the following year.

Field observations over a wide area have shown that Ring Spot is an extremely serious disease of winter lettuce. Several cases were seen in the pandemic season of 1936-37, where whole fields had to be ploughed under, and many others where a large number of the plants had been killed by the disease and the rest rendered so unsightly as to be of little use for market. All varieties appeared to be attacked indiscriminately and it is noteworthy that in the spring of 1937 the healthiest and the worst infected crops seen were both of the variety Lee's Immense. The disease, in some cases, was found to be more severe on specially wet ground, e.g. in one field having a number of springs of water the patches of disease corresponded with the areas soaked by the springs. None the less, badly diseased crops were seen on ground which was well drained.

It is noticeable that if the late spring weather is fine, lettuce plants which were badly infected in the early spring may to some extent grow out of the disease, inasmuch as the fungus does not spread to the newly formed leaves. In 1937, several crops which it had been considered in April were fit only to be ploughed under actually produced useful heads in June. By this time the rain had become discontinuous and the temperature high. Such lettuce is, of course, definitely of second class quality and the outer leaves have to be trimmed off, with consequent reduction in size, and there is a marked tendency for such partially infected plants to wilt very quickly.

The opinion of various growers was sought as to the origin of the disease, and it was found that some thought it came in the seed and some blamed the manure. Experiments now to be described will show that there is justification for both views. The carry-over of the disease, (a) by seed, (b) by trash from an infected crop, (c) by infected weed hosts, was investigated in some detail, and the results will be recorded in this order.

IV. TRANSMISSION OF INFECTION.

(A) By Seed.

Experiments in this connection were carried out in three successive seasons and will be described in chronological order.

1935-36.

Exp. 1. In 1935, three plots of diseased plants, variety Trocadero, and three of clean* plants were kept for seed purposes. Plants which had been badly diseased in the spring made good hearts, the outer leaves of which were

* Throughout the remainder of this paper the term " clean " is used to describe plants (or seed from them) which had not shown Ring Spot disease at any period of growth.

badly holed and marked, but later sent up strong flowering stalks. In July, at flowering time, it required close observation to reveal any difference between the good and the bad lots, although earlier in the season the contrast had been striking. The rise in temperature and the reduction in rainfall as the season progressed arrested the disease. In a few cases lesions were found on the upper stalks, and holes in the upper leaves, but generally, only the old leaves at the base of the plant showed any symptoms. These leaves had all become dried up like brown paper by the time the seed was harvested, thus giving little indication of the earlier state of disease.

The crops were sprayed with Bordeaux mixture, the first application being made when the plants started to bolt, a second just before the flowers opened and a third after the seed had set. The six kinds of seed were from the following:—

I.	Clean	Trocadero	plants,	sprayed	once.
II.	,,	,,	,,	,,	twice.
III.	,,	,,	,,	,,	three times.
IV.	Infected	,,	,,	,,	once.
V.	,,	,,	,,	,,	twice.
VI.	,,	,,	,,	,,	three times.

No difference could be detected on microscopical examination between any of these lots of seed and the germination of all, when tested on damp blotting paper, was equally good. Attempts to isolate Marssonina from lots IV, V and VI failed.

In the second week of September six plots, separated from each other as far as possible and either on newly broken ground or on ground that had not carried lettuce for a long time, were sown with these six kinds of seed in the way ordinarily done for commercial winter lettuce. A seventh plot of commercial seed of the same variety was included in the series. The seed germinated equally well in all plots. Microscopical examination of seedling samples showed that a few from each plot had small brown lesions on the hypocotyls. No Marssonina was obtained from these when isolations were attempted and they are thought to have been either arrested Rhizoctonia lesions or due to some kind of mechanical injury. Seedlings with such marks on the stem were pricked out in boxes and kept under close observation, but the lesions did not extend or cause obvious injury to the plants.

At the beginning of November, after cool, wet weather had set in (see Figs. 1 and 2), lots IV, V and VI quickly became diseased, the cotyledons and, later, the first rough leaves, showed typical perforation. When the disease was first seen in lot IV, about half the plants showed shot-holes, whereas in plots V and VI there were twenty and twenty-six initial groups of infected plants,

respectively, per plot of about one thousand seedlings. Throughout November and December the disease increased in these three plots, IV being definitely worse than either V or VI. Many of the seedlings became completely destroyed as the fungus spread to all the green parts and finally to the growing apex.

By the end of January 1936, the condition of the plots was as follows: There were some twenty survivors in plot IV, and less than one hundred each in plots V and VI. All were severely infected. The seventh plot, sown with commercial seed, had developed some ten diseased patches, plots I and II each showed one patch (containing about twelve plants), while plot III was free from disease. Some diseased plants were found at one spot in plot III by the end of February, and these were removed. In March, there was an occasional diseased survivor in plots IV, V and VI; the plot from commercial seed showed more than 75% of the plants severely attacked, plots I and II had considerable disease but less than the preceding, while plot III was clean except for one small patch of spotted plants.

Transplantings were made from plot III and from the plot from commercial seed. The former produced a first-class clean crop. The best seedlings available were taken from the latter, some of them apparently clean, but the whole crop when hearted was badly diseased and worthless.

The foregoing results clearly indicate that the disease is seed-borne, and in particular that the commercial stock of seed was intermediate between the better and the worse lots of seed which had been produced at Slough. The spraying treatments obviously had some effect, but in the long run it was only the seed from the three times sprayed clean mother plants which produced a satisfactory crop. So far as could be determined, the primary infection of the plot from commercial seed began in about ten places. Assuming that each of these arose from one initially infected seedling, the effective contamination of the seed was very low, viz. less than 1% of the seed sown. Nevertheless, under the conditions prevailing, this slight initial infection was sufficient to render the final crop entirely unsaleable.

Exp. 2. Sowings were made in November 1935 in cold frames with seed types I, IV, V and VI as described on page 35. Each batch of seed was used (a) untreated, (b) treated with Ceresan,* (c) treated with Uspulun and (d) watered in with Cheshunt Compound. The frames were kept as dry as possible to minimize trouble from Botrytis. Apart from injury caused by Ceresan, germination was good in all cases, and no Marssonina appeared. The plants were transferred to the open ground at the beginning of April and by mid-June had hearted up, remaining free from Ring Spot disease to the end. It was very striking that a clean crop could be obtained under the conditions of

* Details of seed treatment are discussed in a later section.

frame cultivation from seed (IV, V and VI) which, in the open field, gave speedy and total failure.

Exp. 3. Boxes of soil were sown with seed of type IV (i.e. of that which gave the worst performance in the field) in a heated greenhouse (temperature ranging round 20° C.) and maintained there during December-February. Though the boxes were liberally watered, no Ring Spot disease developed. The importance of a low temperature is therefore emphasized.

Exp. 4. Seed of type IV was sown in January in pots of soil and maintained in a cool room (temp. range 6-15° C.). The seed was either (a) untreated or treated with (b) 0·1% mercuric chloride solution, (c) 10% bleaching powder solution, (d) 1% formalin solution, (e) Uspulun solution, (f) Ceresan dust, (g) Cheshunt Compound solution. Injury was caused by mercuric chloride, Ceresan and formalin. Ring Spot disease appeared only on the control plants and on those which had been treated with Cheshunt Compound, but the experiment had to be discontinued prematurely on account of severe damping-off.

Exp. 5. The preceding experiment was repeated in March in field sowings. All plants, from treated or untreated seed, were free from Ring Spot disease.

Exp. 6. Untreated seed of type IV was sown in the open at the end of July and liberally watered. No disease was seen until October when it developed on the lowermost leaves of the plants, which, by then, were fully grown and had hearted. This experiment shows that the disease may lie latent, if the conditions are unfavourable to it, and develop some months later when cold, wet conditions supervene.

1936-37.

In 1936, seed was saved from (1) clean Market Favourite and (2) diseased Trocadero plants, neither having been sprayed. This seed, together with certain residues from that of the previous year and with commercial seed, was used in a series of experiments which were carried out on a larger scale and at a number of centres.

Exp. 1. Outdoor plots were sown on October 12th at Slough with the following:—

A. Clean Market Favourite, untreated.
B. ,, ,, ,, treated bleaching powder.
C. Infected Trocadero 1936, untreated.
D. ,, ,, ,, treated bleaching powder.
E. ,, ,, 1935, untreated.
F. ,, ,, ,, treated bleaching powder.

By November 20th severe Marssonina damage was evident in plots C and E, most of the seedlings showing holes in the cotyledons and first leaves. The plots D and F were not entirely free from trouble, though showing a great improvement over the untreated. Some twenty-four seedlings in each of these plots were infected. By December 1st there were many blanks in C and E, only about half the seedlings surviving, and these being badly diseased. In D and F there was still a good stand of plants, but a quarter of each plot showed some disease. Plots A and B were clean at this date. At the beginning of March only a sprinkling of plants was left in C and E, whereas D and F showed fair stands of plants, all of which were infected. In A and B there were two groups of diseased plants, each involving about twenty plants. In April the plants from plots A and B were lifted, when it was found that almost half from each plot were infected. Apparently clean plants from A were selected and planted out and they gave a crop which had 11% of slightly infected plants at the time the crop was cut on June 24th.

Exp. 2. On September 23rd four plots were sown in drills at a farm in Hounslow, as follows:—

A. Clean Market Favourite (Slough seed).
B. ,, ,, ,, treated bleaching powder.
C. Commercial Winter King.
D. ,, ,, ,, treated bleaching powder.

Germination was good on all the plots. One-third of each was sprayed with Bordeaux mixture (3:6:50) and one-third with sulphur-resin spray, on November 25th and December 31st. None of these applications caused any damage. Ring Spot disease was detected on March 3rd, when a few plants in plot C were seen to be infected. These were rogued out together with all the neighbouring plants, so that approximately one foot length of the drill on each side of the infected patch was cleared. Of the remaining plants, half were lifted and planted and the other half were thinned out during the first week in April. Those not transplanted were ready to be cut at approximately the same time as those which had been lifted and replanted. The latter showed some check after planting but later made better growth, probably because the ground under them had been worked more recently. All were free from disease.

Exp. 3. On October 23rd plots were sown broadcast at a farm in Heston with the following seed:—

A. Commercial Market Favourite.
B. ,, ,, ,, , treated bleaching powder.
C. ,, Imperial.
D. ,, ,, , treated bleaching powder.

All germinated well and the seedlings were clean. Spraying was carried out as in the previous experiment and on the same dates. Marssonina was first seen on November 25th in a patch of some twenty plants in plot A, all the rest being apparently clean. By January 27th Ring Spot was rampant in the untreated unsprayed Imperial sub-plot, and the corresponding batch of Market Favourite had two diseased patches involving about one-third of the total plants. Each sprayed untreated plot was clean as were also all the treated plots (B and D).

On January 27th, 204 seedlings from each sub-plot of Market Favourite were transplanted to fresh ground, and on June 3rd these gave the results shown in Table I.

TABLE I.

Plot.	Seed.	Spraying.	Survivors.	Diseased.
A1	Untreated	None	167	92
A2	,,	Bordeaux	187	27
A3	,,	Sulphur-resin	192	22
B1	Treated bleaching powder	None	189	34
B2	,, ,,	Bordeaux	178	12
B3	,, ,,	Sulphur-resin	173	29

The outstanding result is the high degree of infection in the unsprayed plants from untreated seed.

The plants of Imperial (C and D) were left to overwinter in the seed-beds. On March 14th, when spraying was repeated, the plants were very crowded and their appearance at that date was as shown in Table II.

TABLE II.

Plot.	Seed.	Spray.	Condition of plants on March 14th.
C1	Untreated	None	All plants badly diseased; whole plot brown.
C2	,,	Bordeaux	Majority of plants showing perforated leaves; plot green.
C3	,,	Sulphur-resin	,, ,, ,,
D1	Treated	None	All plants appearing clean.
D2	,,	Bordeaux	,, ,,
D3	,,	Sulphur-resin	,, ,,

These results again indicate an improvement—in this case pronounced—from seed-treatment, and also some check on the disease by spraying the seedlings.

A batch of 800 seedlings from plot D was transferred to a farm in Surrey where they produced a good crop of lettuce (and later of seed), and this in a season when all commercial crops of this variety seen by the author were very badly diseased.

Exp. 4. On October 13th, 1936, frames were sown at Slough with seed, untreated and treated with bleaching powder solution, of commercial Market Favourite, commercial Imperial, clean Market Favourite and infected Trocadero. A few diseased plants were found at various times throughout the winter in the frame sown with untreated infected Trocadero seed, and though all visibly diseased seedlings were discarded at the time of transplanting, there was a general though slight infection of the mature crop. All the other batches remained free from Ring Spot disease throughout.

Exp. 5. On November 4th, eight boxes were sown with infected Trocadero seed and placed in the open. Two were left uncovered and the other six were protected by large sheets of glass raised six inches above the soil surface. There was free access of air under the glass, so that the boxes were protected from rain but had practically the same temperature conditions as the outdoor plots. On December 11th the glass was removed from two of the boxes and on January 12th from two others. The boxes which were exposed from the beginning of the experiment gave poor germination, the seedlings became infected on the cotyledons and were all destroyed by Marssonina by the end of December. The first lot to be uncovered showed holes in the seedling leaves ten days later, but the second lot remained apparently clean until February 12th. The seedlings kept continuously under glass remained free from the disease.

1937-38.

In the summer of 1937 seed was saved from clean lettuce of the following varieties: Feltham King, Winter King, Imperial, Improved Trocadero and the previous year's infected Trocadero, which had given clean plants from treated seed in frames. All these lots of seed-mother-plants were sprayed six times. Seed was also saved from diseased Improved Trocadero and Imperial (not sprayed) and, as in the preceding summers, good yields were obtained from all. The germination of infected and clean seed was equally good. Repeated attempts to isolate Marssonina from the seed from diseased plants again failed.

Exp. 1. Sowings of all the above lots of clean seed were made between September 3rd and September 12th at Slough, Reading and Hounslow. The plots remained free from disease throughout.

Exp. 2. Sowings of diseased Imperial seed were made at Reading on September 3rd after the following treatments: (a) untreated; treated with (b) bleaching powder, (c) cuprous oxide dust, (d) zinc oxide dust, (e) dust containing collodial copper and zinc, (f) Ceresan diluted with two parts talc, (g) ethyl mercury chloride dust. Germination was poor in lots (b) and (f).

By November 24th Ring Spot disease had appeared in lots (a) and (d), and by January was present in all plots except the one treated with bleaching powder.

Exp. 3. Exp. 2 was repeated on a nursery at Slough, with the same results.

Exp. 4. Market Favourite seed from diseased plants was sown on October 8th at Slough, under the same conditions as in Exp. 2. Here again the treatments with Ceresan and bleaching powder gave reduced germination. By November 8th disease was widely spread in the control plot ; the one from seed treated with bleaching powder was clean while all the others showed the disease sporadically. On February 3rd there were only five maimed plants surviving in the untreated lot and although most of the plants were surviving in the dust-treated plots, they were all infected with Marssonina. There was also one small patch of disease in the plot treated with bleaching powder, but this may have spread from a neighbouring diseased plot.

Exp. 5. Diseased seed of Lobjoit's Cos was sown at Slough on August 28th with the same set of treatments as in Exp. 2. By November 2nd disease had appeared in all the plots except the one treated with bleaching powder. This experiment was discontinued on account of frost damage.

Exp. 6. A late sowing (November 17th) was made at Slough of Imperial and Market Favourite, clean and diseased, the latter untreated or treated with (a) bleaching powder and (b) methylated spirit. Germination of all was poor and slow. On February 5th a few spotted seedlings were seen in the plots from untreated diseased seed of both varieties. As the late winter and spring were unusually dry the disease made no appreciable progress.

Exp. 7. Commercial seed of Lee's Immense, MacHattie's Giant, Winter White, Arctic King and Stanstead Park, with or without bleaching powder treatment, were sown at Slough on September 20th. By the end of the year disease had appeared in the untreated plots of the first two. At the beginning of March there was sporadic disease in all the untreated plots except Winter White, while all the treated ones were free from disease. In the dry season which followed, all lots outgrew the disease.

Exp. 8. On October 7th sowings were made of commercial and of clean Imperial seed. Disease showed up in the former by December 11th. These plots were abandoned on account of injury from frost and birds.

It was evident from all the field experiments enumerated above that Marssonina could be borne readily on the seed from diseased plants. Conclusive proof of this was obtained when diseased and clean seed of Imperial and Market Favourite varieties was sown in pots of sterilized soil which were

put outside under belljars and kept well watered with sterile water from November 1937 to January 1938. There were six pots of each lot and Ring Spot appeared in two of those sown with infected Market Favourite and one sown with infected Imperial. No disease occurred in the plants from the clean seed.

It has been found throughout this work that when infected seed germinates under cool moist conditions, the stand of seedlings may be good but the cotyledons become perforated at an early stage. On the other hand, when germination takes place under warm or dry conditions, similar seed produces apparently clean seedlings ; nevertheless, when these are later subjected to cool wet conditions the disease appears. There may thus be a latent period, the limits of which are unknown, but as the following experiment shows, it may extend to about two months.

Twelve pots were sown with clean Imperial seed, and as soon as the cotyledons had expanded, each was inoculated with a drop of a spore suspension of Marssonina spores. The pots were kept cool and moist under belljars out of doors for a time, then warm and dry in a heated greenhouse (15-20° C.), and finally out of doors once more. The progress of the experiment was as given below, the observations corresponding to each period being given in brackets :—

(1) Four pots, outside, January 4th-7th (no disease shown) ; inside, January 7th-March 1st (no disease shown) ; outside, March 1st-23rd (typical symptoms).

(2) Four pots, outside, January 4th-14th (small brown specks produced) ; inside, January 14th-March 1st (as before) ; outside, March 1st-23rd (typical symptoms).

(3) Four pots, outside, January 4th-21st (perforation of cotyledons and majority of seedlings killed) ; inside, January 21st-March 1st (lesions still visible but not extending) ; outside, March 1st-23rd (disease spreading).

(B) By Trash.

Salmon and Wormald (14) attributed the epidemic of 1922 at Swanley to diseased trash brought in with the manure. Brandes has shown that viable spores may be present in diseased leaves after 2½ months. The following experiments were carried out to investigate the question of trash transmission.

Exp. 1. In September 1935, clean seedlings were planted in boxes with the soil of some of which diseased leaves had been incorporated. They were kept outside and well watered. By November Marssonina appeared on the plants in the boxes to which diseased material had been added but not on those in the controls.

Exp. 2. In March 1936 three plots were planted with winter lettuce seedlings raised from clean Trocadero seed as follows:—

(1) on newly broken ground,

(2) on a plot which had carried diseased lettuce in the spring of 1935,

(3) on a plot in which diseased plants had matured seed in the summer of 1935.

No disease appeared in any of these plots and good clean lettuces were cut by the middle of June. The weather following planting was suitable for the development of the disease, which was present on other infected plots during the same period.

Exp. 3. Simultaneously with the above experiment, two plots were planted with clean Trocadero seedlings: (a) on fresh ground; (b) on a plot where diseased seedlings had died out in the previous January. At the time of hearting (a) gave clean plants and (b) gave 30% slightly infected. This result indicates that the fungus is able to persist on the trash of a previous crop for two months at least.

Exp. 4. Sowings of Market Favourite made in the spring of 1937, under conditions similar to those of Exps. 2 and 3, confirmed the fact that the disease could be transmitted from trash over a period of some 2-3 months, but not over one of 8 months, after a diseased crop had occupied the ground.

The writer's field experience in the neighbourhood of London is in agreement with the view that the trash from a diseased crop does not remain infective for a very long time, for example, over summer. The planting of an autumn crop on land which bore a diseased crop in the preceding spring has not led to any abnormal outbreak of disease. On the other hand, in some districts where a close rotation is practised, e.g. around Cheltenham, the disease is found to recur on the same spots. This could be interpreted as meaning that the conditions of soil moisture and atmospheric humidity in such spots were specially favourable for the development of the disease (from seed-borne infection ?) or that the fungus persisted in the soil. It is known that the fungus produces chlamydospores in old lesions and these must pass into the ground, but there is as yet no information as to their viability or capacity to produce infection.

While, therefore, it has been clearly shown that Ring Spot disease may be transmitted from infected trash, the latter loses its infectivity in a fairly short time (eight months or thereabouts), but it is possible that this period may be longer under certain local conditions.

(C) By Weeds.

As was stated in the introductory section, *M. Panattoniana* had been found on a weed (*Lactuca Scariola*) in America. In 1932 a species of Crepis (Hawksbeard)* growing in the experimental plots at Slough had been observed to be infected by a fungus resembling Marssonina, and in 1937, infected plants were numerous. It was further noticed that the disease was confined to plants growing on plots which were carrying or had recently carried diseased crops of lettuce. Symptoms of the disease on Crepis include typical shot holes and small lesions on the midrib, but the most marked effect is a severe twisting and distortion of the leaf.

Isolations of the fungus from Crepis gave cultures which showed only minute differences in cultural features from that from lettuce. Whereas, however, it has proved easy to transmit the lettuce and Crepis isolates to their respective hosts, cross inoculations by a variety of methods have failed in all but one of the attempts. The distribution of diseased Crepis plants in the Slough plots is strongly suggestive of passage of the fungus from lettuce to Crepis, but the evidence so far is that the two races are biologically distinct, though under peculiarly favourable conditions the one may be able to infect the host of the other. Further work will be necessary to determine the significance of the strain on Crepis in connection with the Ring Spot disease of lettuce.

V. VARIETAL RESISTANCE.

Field observations frequently show that some varieties of lettuce are more severely attacked than others and thus growers tend to claim that there is some degree of varietal resistance to the disease. Controlled experiments have failed to indicate any appreciable differences in the varieties tested. Thus, under cool, moist conditions in frames, spraying the young plants with a water suspension of Marssonina spores produced severe disease in the varieties Imperial, Market Favourite, Early French Frame and Gotte Blanche, which are respectively typical winter, spring and (the last two) frame varieties. In practice the first-named variety is often severely attacked, the last two, in the writer's experience, not at all. This difference is obviously due to the different methods of cultivation and not to any inherent difference in resistance.

A similar experiment, carried out over winter in frames with the varieties: Improved Trocadero, Feltham King, Winter King, Arctic King, Stanstead Park, Imperial, MacHattie's Giant, Lee's Immense, Winter White and Lobjoit's Cos, gave infection ranging from 75-100% of the seedlings. Under these conditions all the varieties are highly susceptible.

* *C. capillaris* Wallr. (= *C. virens* auct.), kindly identified by Mr. A. J. Wilmott of the British Museum (Natural History).

In the spring of 1937 plots of clean seedlings of Trocadero, Market Favourite, Imperial and Winter King were interplanted in a comparable manner with diseased seedlings of Market Favourite. No difference was noted in the rate of spread of disease to the clean plants of these four varieties.

Field observations made over a wide area during the two seasons 1936-37 and 1937-38 showed that all the above-mentioned field varieties were severely diseased at one farm or another. In a number of cases it was possible to confirm the observation that the severity of the disease in the field was correlated with the amount of disease shown earlier in the seed bed. The variations which occur from place to place are to be set down to some extent to details of cultivation and to local soil conditions, but more particularly to infection from the remains of a recent, infected crop and to variations in the quality of the seed. Since nearly all the commercial seed is grown abroad, it has not been possible to determine why some batches of it are less contaminated with Marssonina than others.

VI. SEED DISINFECTION.

The use of bleaching powder for seed disinfection was first described by Wilson (17) and advocated as showing a wide margin of safety. Later, White (16) came to the same conclusions. In much of the present work, as shown in Section IV, this substance has been used and invariably with beneficial effect in reducing the incidence of Ring Spot disease. In some cases the disease was in effect eliminated by this treatment, but in others (as in Exp. 1 of 1936-37, p. 37), though there was a marked improvement in the early stages, the degree of control proved inadequate in the long run. It is obvious that the treatment would not affect such seeds as might be infected internally as apart from those which are merely contaminated on the surface.

The method of preparation was as follows:—

Bleaching powder was well mixed with ten times its weight of water and left to settle for about half an hour. The almost clear supernatant liquid was strained off through muslin. Lethalate wetting compound, which was the only reagent tried which did not cause precipitation, was added at the rate of 0·5 gm. per litre.

Extensive experiments with seed of sixteen of the commonly grown varieties showed that the method of treatment was safe, i.e. there was no material reduction in germination, if the duration of treatment did not exceed twenty-four hours and if the temperature was kept below 25° C. As a measure of precaution it is recommended that the period of immersion should be reduced to 4-6 hours. It is important, however, that treated seed be sown as soon as possible after treatment as it loses its germinative capacity quickly on storage.

The bleaching powder method has further disadvantages. As it is a wet treatment, involving at least several hours' immersion, it is necessary to dry the seeds before they can be sown by the drill or even by hand. A more important objection is the variability in composition of commercial bleaching powder, and this is probably responsible for the occasional bad effects produced on germination (see Exps. 2-4, pp. 38-40).

Wilson states that the solution used by him contained approximately 2% of available chlorine. The commercial samples tested by the writer gave the following amounts of available chlorine per 10% solution:—

Brand B	1·6%
,, T	1·2%

A 5% preparation of Brand B gave 1·4% of available chlorine, i.e. not appreciably less than did a 10% solution.

It does not appear, however, that the percentage of available chlorine gives a trustworthy index of the safety of a solution. Thus, whereas solutions of bleaching powder containing 1-2% of available chlorine nearly always proved to be safe, more or less severe injury was produced by "Chloros", a stabilized chlorine water, even when diluted so as to contain only 0·5% available chlorine, and also by a solution of sodium hypochlorite containing as little as 0·2% available chlorine. Further knowledge of the mechanism of the disinfection process and further standardization of the commercial material are required before the method can be recommended as free from risks.

As shown above (p. 40) attempts to replace the bleaching powder solution method by dry dusting treatments were not successful. Mercurial dusts have shown harmful effects, even when diluted with talc, and others, though not harmful, have given unsatisfactory control of the disease.

Treatment of the seed with methylated spirit for a period up to six hours, alone or with 0·1% iodine added, has been found to give no material depression of germination, and this method has the advantage that the seed does not become swollen and therefore is easily dried. The fungicidal value of this treatment has, however, not yet been tested.

Attempts were made to devise a hot water treatment for lettuce seed, but the results were very unpromising.

VII. CONTROL MEASURES.

In the light of the results given in the foregoing sections the following recommendations may be given:—

1. Winter lettuce should not be sown or planted on ground which has recently borne a crop infected with Marssonina. Crops of lettuce maturing

in the late autumn often show Ring Spot damage, and to attempt to grow a winter crop immediately following such a crop is to risk a severe outbreak. On the other hand, it is probably safe to grow a winter crop on land which has not borne lettuce from midsummer onwards, i.e. so far as carry-over of the disease by infected trash is concerned.

2. Spraying a seedling crop with Bordeaux mixture (3 : 6 : 50) is not harmful under winter conditions, and materially checks the onset of disease. If, therefore, the crop is grown in seed beds until January or February, control by spraying is practicable. Lettuce treated in this way may mature later than autumn-planted lettuce, but the stand of plants would be fuller and there would be less infection with Marssonina.

3. The use of clean seed is undoubtedly the most important single factor, and though the present work has shown that stocks of seed which are much superior to the commercial can readily be produced on an experimental scale, the position at the moment is that commercial seed is liable to carry the disease and to give in a suitable year a severely infected crop. Until such time as clean seed is obtainable in quantity, the grower can be recommended to treat the seed of his winter lettuce crop by the bleaching powder method (see p. 45).

VIII. DISCUSSION.

A striking point which emerges from the experiments described above is the long latent period (about two months) which may elapse from the sowing of infected seed to the appearance of typical symptoms of Ring Spot. It may be suggested that spores present on the seed-coat (and therefore carried up above ground by the seedlings) come in contact with the cotyledons and remain there ungerminated, but viable, for a considerable time. Alternatively they may germinate and produce attachment organs, which in this type of fungus are known to be long-lived and resistant. When, later, conditions become more favourable for the fungus, attack takes place. There is the further possibility that some of the late and slight infections which occurred in plots raised from supposedly clean seed (e.g. in Exp. 1, p. 34) were due to accidental transmission from diseased plots by agents such as insects, birds or workers' tools.

It would be expected *a priori* that seed from diseased plants would carry fungus spores. Pape's (12) definite assertion to the contrary is not easy to understand. If the leaves and stems carry freely sporing lesions and such plants are pulled or cut and made into stacks and subsequently threshed—as is the commercial practice—there is every probability that the seed will become contaminated with spores. There is also a small residue of trash among the seed and a certain percentage of this is likely to have broken away from the

edges of old lesions containing mycelium and chlamydospores. With the bad seed used in the experiments described in Section IV, it is suggested that so many spores were present that some were bound to germinate at the first suitable time, so that infection occurred at an early stage in development. Even in this example, however, the indications were that only a certain proportion of the plants became initially infected ; that is to say, that in only a limited number is the successful transfer made from seed-coat to cotyledon and this followed by germination, penetration and disease.

An apparent flaw in the argument for seed-transmission of the disease is that the fungus has not yet been isolated from the bad seed. The difficulty in making such isolations is that Marssonina grows very slowly and that other organisms which develop rapidly are present on the seed. Success in this matter would appear to depend on separating Marssonina from the other fungi and bacteria associated with it.

IX. SUMMARY.

1. Ring Spot of lettuce, the symptoms of which are described, is an important disease of winter lettuce in England, in many seasons causing a heavy reduction in the quantity and quality of the crop. It rarely occurs, if at all, on lettuce which is headed out under glass and it is of subsidiary importance on lettuce grown over winter in frames and planted out in spring.

2. Experiments over three seasons have shown that the disease is readily transmitted by the seed. The freedom or otherwise of the seed-mother-plants is strongly reflected in the behaviour of the crop from the ensuing seed. Diseased plants produce seed of high germinating capacity and free from surface blemish. Nevertheless, under suitable conditions, which are often realized in autumn sowings, such seed gives a heavily infected crop which may be completely destroyed by the disease. At the opposite extreme, seed has been obtained from sprayed and segregated mother plants which has given a crop almost completely free from disease under conditions where commercial seed gave heavily diseased and valueless crops.

3. The disease may also be contracted from the remains of a previous infected crop, and the measure of the danger of this source of contamination has been roughly assessed.

4. There is some evidence that a commonly occurring weed (*Crepis capillaris* Wallr.) may perhaps act as a source of infection.

5. Under comparable conditions, all the commercial varieties tested (sixteen altogether) are highly, and as far as could be determined, about equally susceptible to Ring Spot disease.

6. Reduction of the disease in commercial crops is effected by spraying the seedlings with Bordeaux mixture and by treatment of the seed with a solution of bleaching powder. The latter method is not entirely safe but is reasonably so if certain precautions are adopted. None of the seed-dusting treatments tried proved to be of value.

7. Under certain conditions the disease may remain latent in a seedling crop for a considerable time, two months at least. An explanation of this behaviour is suggested.

ACKNOWLEDGMENTS.

The author wishes to thank Professor W. Brown for his help and guidance throughout the work, and also many growers and seedsmen who rendered valuable help by allowing their crops to be examined. In particular the following growers and seedsmen gave facilities for experimental work to be done on their farms: Mr. W. Barker, Laleham ; Messrs. Gray Bros., Heston ; Mr. F. A. Secrett, Walton-on-Thames ; Messrs. Sutton and Sons, Reading and Slough ; Messrs. Robbins and Sons, Heston and Hounslow. The work carried out over the period 1936-38 was made possible by a grant from the Agricultural Research Council.

REFERENCES.

(1) *Appel, O.* and *Laibach, F.* Über ein im Frühjahr 1907 in Salatpflanzungen verheerendes Auftreten von *Marssonina Panattoniana* Berl. Arb. K. Biol. Anst., Berlin, 1908, **6**, 28.

(2) *Berlese, A. N.* Un nuovo marciume dell' Insalata (*Lactuca sativa*). Riv. Patol. Veg., 1895, **3**, 339.

(3) *Birmingham, W. A.* Anthracnose in lettuce. Agri. Gaz., N.S. Wales, 1927, **38**, 487.

(4) *Brandes, E. W.* Anthracnose of lettuce caused by *Marssonina Panattoniana*. Journ. Agri. Res., 1918, **13**, 261.

(5) *Chittenden, F. J.* On some plant diseases new to, or little known in, Britain. Journ. Roy Hort. Soc., 1912, **37**, 541.

(6) *Dandeno, J. B.* A fungous disease of greenhouse lettuce. Rep. Mich. Acad. Sci., 1906, **8**, 45.

(7) *Kern, H.* Important or new plant diseases observed during 1926-28. Bull. of Plant Protection, 1929, **3**, 82.

(8) *Magnus, F.* Notwendige Umänderung des Namens der Pilzgattung *Marssonia*, Fisch. Hedwigia, 1906, **45**, 88.

(9) *Marchal, F.* and *Foëx, E.* Rapp. Phytopathologique pour l'Année 1913. Maladies des Cultures Maraîchères en 1913. Ann. du Serv. des Épiphyties, 1913, **2**, 31.

(10) *Ogilvie, L.* and *Mulligan, B. O.* Progress report on vegetable diseases. V. Ann. Rep. Long Ashton Res. Sta. for 1933, 1934, 98.

(11) *Oudemans, C. J.* Nederlandsch Kruidkundig Archief, III serie, 2 deel, 297 and 1117.

(12) *Pape, H.* Der Pilz ***Marssonia Panattoniana*** Berl. als Schädling des Samensalates. Gartenbauwissenschaft, 1929, **1**, 524.

(13) *Parker, C. H.* Notes on Anthracnose of lettuce. Phytopath., 1923, **13**, 510.

(14) *Salmon, E. S.* and *Wormald, H.* The "Ringspot" and "Rust" diseases of lettuce. Journ. Min. Agri., 1923-24, **30**, 147.

(15) *Selby, A. D.* Investigations of plant diseases in forcing house and garden. Lettuce leaf perforation. Ohio Agri. Exp. Sta. Búll. 73, 1896, 222.

(16) *White, H. L.* The sterilization of lettuce seed. Exp. Sta., Cheshunt, Ann. Rep. for 1934, 1935, 41.

(17) *Wilson, J. K.* Calcium hypochlorite as a seed sterilizer. Am. Journ. Bot., 1915, **2**, 420.

(18) *Wortley, W. R. S.* The effect of salts of Lithium on the resistance of certain plants to disease. Journ. Roy Agri. Soc., 1936, **97**, 492.

(*Received* 2/12/38.)

INCOMPATIBILITY AND STERILITY IN THE GAGE AND DESSERT PLUMS

By **M. B. CRANE** and **A. G. BROWN**
John Innes Horticultural Institution, Merton

INTRODUCTION.

In previous reports on experiments in progress at Merton the occurrence and behaviour of sterility and incompatibility in many varieties of apples, cherries and plums have been described. The last detailed report on the work with plums was published in 1925. The experiments have been continued under the same methods of control as were described in earlier papers, and in the present account are given the results obtained from an investigation of the Gage group and other dessert varieties. The culinary varieties, President, Rivers' Early Prolific and Victoria, are included to show their reactions with dessert varieties, and particularly the interaction of President with varieties in the Gage group ; but in general, the results of the work with culinary varieties and with families of seedlings raised from various self- and cross-pollinations are withheld.

The varieties used in the experiments and the results obtained from the cross-pollinations made are given in the appended Table VI. In it the varieties are arranged in alphabetical order. Cross-incompatible and partially cross-incompatible pollinations, when they occur, are detailed at the beginning of the columns and are printed in italics. Then follow the results obtained from inter-varietal compatible pollinations, and finally, at the ends of the columns, the results are given of pollinations between plums of the domestica group with the sloe, *Prunus spinosa,* and the cherry plum, *Prunus divaricata.* The numbers of fruits recorded in this and in all other Tables are the numbers which reached maturity.

The terms " self-incompatibility " and " cross-incompatibility " are used in this account, as in previous papers, since they are more precise and accurate than the terms " self-sterility " and " cross-sterility ".

SELF-POLLINATIONS.

The results given below are those obtained from self-pollinations. They show that the varieties can be grouped provisionally into three classes, as follows :—

(1) Varieties which are completely self-incompatible and which entirely fail to set fruit with their own pollen.

	Flowers Self-pollinated.	Fruits matured.	Per cent. matured.		Flowers Self-pollinated.	Fruits matured.	Per cent. matured.
Allgrove's Superb ..	933	1	—	Jefferson	1,515	1	—
Bryanston Gage ..	737	0	0	Kirke's Blue ..	1,229	0	0
Coe's Golden Drop ..	1,668	2	—	Late Orange ..	2,283	0	0
Coe's Violet ..	1,426	0	0	McLaughlin's Gage ..	891	1	—
Comte d'Althan's Gage	771	1	—	Old Greengage A. ..	1,431	1	—
Crimson Drop ..	470	1	—	Old Greengage B. ..	1,662	1	—
Decaisne	648	1	—	President	2,185	1	—
Early Greengage ..	2,141	0	0	Transparent Gage ..	1,222	3	—
Golden Esperen ..	—	—	—				

(2) Varieties which are only slightly self-compatible and are incapable of producing a satisfactory crop with their own pollen.

	Flowers Self-pollinated.	Fruits matured.	Per cent. matured.		Flowers Self-pollinated.	Fruits matured.	Per cent. matured.
Blue Rock	4,102	30	0·7	Old Greengage D. ..	612	2	0·3
Cambridge Gage ..	9,461	98	1·0	Rivers' Early Prolific	25,419	868	3·4
Old Greengage C. ..	882	25	2·8				

(3) Varieties which are self-compatible and which can develop full crops with their own pollen.

	Flowers Self-pollinated.	Fruits matured.	Per cent. matured.		Flowers Self-pollinated.	Fruits matured.	Per cent. matured.
Denniston's Superb ..	2,030	950	46·8	Laxton's Gage ..	2,603	308	11·8
Early Transparent Gage	1,327	623	46·2	Oullin's Golden Gage ..	908	349	37·3
Golden Transparent Gage	588	330	56·1	Reine Claude de Bavay	490	79	16·1
Guthrie's Greengage ..	1,541	367	23·8	Victoria	12,499	3,544	27·5

The results obtained from self-pollinations of the varieties in these three classes are summarized in Table I.

TABLE I.

Class.	No. of flowers self-pollinated.	No. of Fruits matured.	Per cent. matured.
1	21,212	13	0·06
2	40,476	1,023	2·53
3	21,986	6,550	29·79

It is possible that the few fruits which set in Class 1 following self-pollination are the result of error, i.e. due to accidental cross-pollination ;

but the possibility of a self pollen-tube, as a rarity, travelling the length of the style and effecting fertilization cannot be precluded. In Class 2 the average set was only 2·53 per cent. Amongst the individual pollinations made in this class, some resulted in a higher and some in a lower set of fruit, but, as can be seen from the details given in Table VI, all the varieties in both Class 1 and Class 2 are dependent on cross-pollination for the production of satisfactory crops.

Amongst the varieties in Class 3 the average proportion of fruit which reaches maturity following self-pollination varies considerably. Thus, taking the extremes, the average set of Golden Transparent is 56·1 per cent., whilst that of Laxton's Gage is only 11·8 per cent. As shown in Table VI, Laxton's Gage and also Reine Claude de Bavay have set a higher proportion of fruit from certain cross-pollinations, but in individual self-pollinations all the other varieties in Class 3 have set as high a proportion of fruit as they have in any cross-pollination. For example, the variety Victoria has been selfed on several different occasions and has given an average set of 27·5 per cent., but in individual self-pollinations it has given a set of over 70 per cent. Probable causes of variation in the proportion of fruit set following the same pollination are discussed later, but the results show that Laxton's Gage and Reine Claude de Bavay may set a heavier yield following certain cross-pollinations than when self-pollinated. The other varieties in this class, however, can set fruit as freely with their own pollen as when cross-pollinated.

CROSS-POLLINATIONS.

As with the results obtained from self-pollinations, those from cross-pollinations can be provisionally arranged in three classes: (1) Cross-incompatible pollinations ; (2) Partially compatible cross-pollinations ; (3) Compatible cross-pollinations. The total results are summarized in Table II.

TABLE II.

	Flowers cross-pollinated.	Fruits matured.	Per cent. matured.
1. Incompatible cross-pollinations ..	8,387	8	0·09
2. Partially compatible cross-pollinations	5,792	111	1·91
3. Compatible cross-pollinations	51,950	15,754	30·32

The proportion of fruit set from cross-pollinations in these three different classes is very similar to that set in the three corresponding classes from self-pollinations in Table I. It is probable that the few fruits which set in the incompatible cross-pollinations may be the result of error, but as in the self-compatibles the possibility of an occasional pollen-grain functioning cannot be

entirely precluded. The co-incompatible varieties, the groups to which they belong and the effective and non-effective pollinations are shown in Table III.

It will be seen from Table III that in all cross-pollinations where self-compatible varieties have been used, either as males or females, the pollinations were always effective. It therefore follows that cross-incompatibility has

Table III.

♀ \ ♂	Allgrove's Superb	Jefferson	Coe's Golden Drop	Coe's Violet	Crimson Drop	President	Late Orange	Old Greengage 'A'	Old Greengage 'B'	Old Greengage 'C'	Old Greengage 'D'	Cambridge Gage	Rivers Early Prolific	Blue Rock	Bryanston Gage	Comte d'Althan	Decaisne	Early Greengage	Golden Esperen	Kirke's	McLaughlin's Gage	Transparent Gage	Denniston's Superb	Early Transparent	Golden Transparent	Guthrie's Green Gage	Laxton's Gage	Oullins Golden Gage	Reine Claude de Bavay	Victoria
Allgrove's Superb	—	—	—	—		+	+					+	+			+						+	+			+	+			+
Jefferson	—	—	—	—	—	+	+	+			+	+		+	+	+	+	+			+		+	+			+	+	+	+
Coe's Golden Drop	—	—	—		—	+	+	+		+		+		+	+	+	+				+	+	+	+	+		+			+
Coe's Violet		—	—	—	—	+	+					+	+							+					+					+
Crimson Drop		—	—	—	—			+												+										
President		+	+	+		—	—	+	+	+	+	+	+	+	+	+	+	+				+	+	+	+	+	+	+		+
Late Orange	+	+	+	+		—	—		+	+	+	+	+	+	+	+	+	+		+	+	+	+	+			+		+	+
Old Greengage 'A'		+	+			-¦-	—	—				-¦-	+	+	+	+		+		+			+	+			+	+		+
Old Greengage 'B'					+	-¦-	-¦-	—	—	—	—	-¦-			+	+		+			+								+	
Old Greengage 'C'			+			-¦-	-¦-	-¦-	—	-¦-	-¦-	-¦-			+			+		+			+	+						
Old Greengage 'D'			+			-¦-	—		-¦-	-¦-	-¦-	-¦-			+			+												+
Cambridge Gage		+		+		-¦-	-¦-	-¦-	-¦-	-¦-	-¦-	-¦-	+	+	+	+		+		+	+		+	+	+	+	+	+	+	+
Rivers's Early Prolific	+	+	+	+		+	+	+		+	+	+	-¦-	+	+	+	+				+	+	+	+			+			+
Blue Rock	+	+		+		+	+	+				+	-¦-	-¦-	+	+							+			+	+			+
Bryanston Gage		+				+	+	+	+			+	+		—			+		+	+									
Comte d'Althan	+		+			+	+	+		+		+	+	+		—	+				+	+	+	+				+		+
Decaisne		+					+						+			+	—						+							
Early Greengage						+	+	+	+	+		+			+	+		—						+						
Golden Esperen	+	+	+			+	+	+				+	+			+	+		—								+	+		+
Kirke's	+			+		+	+					+				+				—				+						+
McLaughlin's Gage		+		+			+					+	+					+			—									
Transparent Gage			+				+					+				+					+	—								
Denniston's Superb		+				+		+				+											+		+					
Early Transparent																				+				+						
Golden Transparent						+						+									+				+					
Guthrie's Green Gage			+	+																						+				
Laxton's Gage		+					+	+								+							+				+	+		+
Oullins Golden Gage		+				+										+											+	+		+
Reine Claude de Bavay									+			+				+		+			+								+	
Victoria		+	+			+		+				+										+	+			+		+		+

+ =compatible, -¦-=partially incompatible, and — =incompatible pollinations.

occurred only between varieties which are wholly or partially self-incompatible. Sometimes it is reciprocally expressed, failure occurring in both directions of crossing, but sometimes it occurs in one direction only.

A few varieties of *Prunus insititia*, the damson and bullace, have been used in the cross-pollinations with plums, and, as detailed in Table VI, they

have in most cases resulted in the development of good crops of fruit. The pollinations between varieties of plums, *Prunus domestica,* and varieties of *P. divaricata* and *P. spinosa* in most cases set comparatively few fruits.

THE GREENGAGE GROUP.

The varieties of greengages are more difficult to distinguish than is usually possible with plums. This is probably due to the close resemblance of their characters, and in particular those of their fruits. Although they all have the characteristic greengage fruit shape and colour, and in some degree the distinctive flavour, they differ in minor characters of growth and flavour.

During the course of these experiments we have obtained, under the name of Old Greengage, trees from several different sources. These trees resembled each other inasmuch as the fruits when mature were all yellowish-green in colour and differed little in flavour ; but among them differences in flower and leaf characters, in the relative time of bud and leaf opening and in incompatibility reactions occurred. Finally, we found that these trees were of four kinds, and, as shown in Table III, they were designated as Old Greengage A, B, C and D respectively. The difference between A and B is very slight ; the anthers of B before they dehisce are yellow, in A they are almost orange, with a tinge of red, and after dehiscence the anthers of A are darker in colour than those of B. The differences between A, D and C are more considerable, as shown in Fig. 1. The flowers of A open before the leaf buds unfold, whereas in D the development of the leaves is already advanced at the time of flowering, C being intermediate in this respect. Both C and D have the reddish tinge in the anthers characteristic of B. Other differences are that the leaves of the young growth of A and B are practically green, whilst those of C and D are distinctly brownish-red. Differences also occur in the quantity and length of the epidermal hairs on the leaves and twigs. The fruits vary slightly in shape, those of A and B are less oblate than C and D ; in the fruits of D the suture is deeper and more pronounced and the fruits are not so symmetrical as in the others. (See Fig. 2.) Occasionally the fruits of Old Greengage develop a slight red flush or reddish dots.

Cambridge Gage resembles the Old Greengage more closely than any of the other greengages used in these experiments ; in the development of its flowers and leaves it closely approximates to Old Greengage D and similarly in the early stages of growth its leaves are brownish-red, but its fruits are quite distinct ; when mature they are much more yellow than any of the Old Greengages. Bryanston Gage is most readily distinguished by its larger leaves and fruits, and Early Greengage, sometimes called July Greengage, by its earlier season of maturity ; in this variety also the petals of the flower buds

are distinctly pink, whilst those of all the others mentioned above are white or cream. Reine Claude de Bavay closely resembles the Old Greengages in flavour, but apart from a number of morphological differences it stands out in these experiments by reason of its fairly high degree of self-compatibility.

As shown in Tables III and VI, the Old Greengage group and Cambridge Gage are in all combinations highly incompatible amongst themselves. It is

TABLE IV.

Cross Compatible Pollinations.	No. of Stones.	No. of Good Seeds.	Per cent. Stones with 2 Seeds.	Per cent. Good Seeds.*	Per cent. Germination.
Allgrove's Superb	339	321	0·1	47·3	62·0
Blue Rock	946	883	17·1	46·6	46·3
Bryanston Gage	94	123	34·1	65·4	—
Cambridge Gage	1,079	1,043	0·0	48·3	79·0
Coe's Golden Drop	442	534	34·3	60·4	62·9
Coe's Violet	91	102	31·8	56·0	—
Comte d'Althan's Gage ..	208	215	10·1	51·7	100·0
Crimson Drop	13	12	7·7	46·1	—
Decaisne	197	77	23·3	19·5	—
Denniston's Superb	159	157	0·0	49·3	80·0
Early Greengage	108	106	0·0	49·0	—
Early Transparent Gage ..	46	35	0·0	38·0	—
Golden Esperen	160	123	0·6	38·4	44·4
Golden Transparent	34	34	11·7	50·0	76·5
Jefferson	953	923	0·7	48·4	76·3
Kirke's	213	184	0·0	48·1	74·5
Late Orange	401	313	5·7	39·0	—
Laxton's Gage..	280	250	0·0	44·6	73·8
McLaughlin's Gage	57	35	8·5	30·7	25·0
Old Greengage A.	551	542	0·0	49·2	76·5
Old Greengage B.	108	101	0·0	46·7	85·7
Old Greengage C.	76	76	0·0	50·0	—
Old Greengage D.	61	60	0·0	49·2	—
Oullin's Golden Gage ..	153	141	0·6	46·0	80·8
President	989	742	5·2	37·5	60·1
Reine Claude de Bavay ..	55	63	18·2	57·1	69·2
Rivers' Early Prolific ..	672	244	6·9	18·1	—
Transparent Gage	56	50	0·0	44·6	—
Victoria	512	679	45·5	61·3	68·7
Self-Pollinations.					
Blue Rock	18	9	0·0	25·0	—
Cambridge Gage	85	71	0·0	41·7	—
Denniston's Superb	602	549	0·0	45·1	—
Early Transparent	126	90	0·0	35·7	—
Guthrie's Greengage	269	231	0·0	42·9	65·4
Golden Transparent	69	46	5·8	33·3	—
Laxton's Gage..	349	301	0·0	43·1	46·2
Old Greengage C.	21	18	0·0	42·8	—
Old Greengage D.	2	1	0·0	25·0	—
Oullin's Golden Gage ..	284	250	0·0	44·0	54·5
Reine Claude de Bavay ..	73	68	1·3	46·5	57·3
Rivers' Early Prolific.. ..	231	52	0·4	11·2	—
Victoria	1,234	1,537	31·0	62·1	—

* In this table the per cent. of good seeds is based on the maximum development of two seeds per fruit.

also shown in these Tables that the pollen of President and Late Orange is ineffective on all of these varieties. On the other hand, in the reciprocal pollinations, both President and Late Orange set a full crop of fruit when pollinated by the Old Greengages and Cambridge Gage.

STERILITY.

Degrees of generational sterility are frequently evident in plums, as shown by the existence of a proportion of defective pollen and ovules. On the female side this is seen by the failure of both of the ovules to develop and form good seeds. As shown in Table IV, several varieties have never developed more than one seed per fruit either when selfed or cross-pollinated. At the other extreme, the variety Victoria yields as many as 45 per cent. of two-seeded fruits from cross-pollinations, and 31 per cent. from self-pollinations. In plums fertilization is essential for fruit formation, but it is clear that this form of sterility rarely if ever affects the actual yield of fruit, at least in established varieties. The fruit develops irrespective of the number of good seeds formed. Sometimes the fruit reaches maturity without forming any good seeds, owing to a breakdown of embryonic growth after some initial development.

The variety Golden Esperen is exceptional in being sterile on its male side. It is therefore useless as a pollinator for other varieties. As shown in Table VI, this variety when used as female has, in the majority of cross-pollinations, given a low yield.

THE INTERPLANTING OF VARIETIES.

These experiments show that most of the self-compatible varieties can set very heavy yields with their own pollen, and if desired they can in practice be planted by themselves. As previously mentioned, the varieties Laxton's Gage and Reine Claude de Bavay, which are included in the self-compatible class, have set a heavier crop in certain cross-pollinations than in self-pollinations. No variety in the self-incompatible or partially self-incompatible classes, however, should be planted in isolation either as single trees or in large blocks, and care should be taken to interplant varieties which are mutually compatible and flower at the same time.

The literature relating to the flowering times of varieties of plums cannot be analysed precisely owing to the different methods of recording this character adopted by different investigators. Rawes (7) takes the early flowering variety Grand Duke as the standard of earliness and places the varieties he recorded in order of flowering without giving actual dates. Hooper (6) gives the date on which the flowers begin to open, also the date of full bloom and the period of flowering. There appears to be considerable fluctuation in the actual date

of flowering in different years, but there is, in general, an agreement in the relative times of flowering of the varieties recorded by these and other investigators, and their results, as far as the varieties here dealt with are concerned, are tabulated in Table V. The flowering times of some of the varieties we have used are not on record.

In Table V the varieties are given in order of flowering, and co-incompatible varieties and the group to which they belong are indicated by a Roman numeral. It may be recalled that in these experiments the pollen of self-compatible kinds of plums has always been effective on self-incompatible varieties. Therefore, if both kinds are grown and their flowering times coincide, it might be advantageous to interplant the self-compatibles and the self-incompatibles.

TABLE V.

Varieties of plums, in order of date of full bloom.

0 days	Grand Duke (standard of earliness).
1-4 days after earliest	Rivers' Early Prolific (III). Blue Rock (III). Allgrove's Superb (I). Jefferson (I). Early Transparent. Reine Claude de Bavay. Denniston's Superb. Coe's Golden Drop (I). Coe's Violet (I). Decaisne. President (II). Late Orange (II).
5-8 days	Comte d'Althan's Gage. Old Greengage (II). Bryanston Gage. Golden Transparent Gage. Kirke's. Victoria. Cambridge Gage (II). Laxton's Gage. Early Greengage.
9-12 days	Transparent Gage. Oullin's Golden Gage.

Varieties in the same incompatible group should not be planted together, nor should varieties at the extremes of the Table, as their periods of flowering do not overlap sufficiently to allow of effective cross-pollination.

DISCUSSION.

Sexual incompatibility is common among plants and is due to the failure of the pollen, though good in itself, to effect fertilization. The physiological basis of incompatibility is the relation between the male gametophyte and the female sporophytic tissue. The precise time at which the incompatibility

reaction occurs varies with different species. This is due to the reaction between the pollen and the female tissue occurring in different parts of the female structure, e.g. stigma, style, integuments, etc. As shown by Roy (8) in the domestic plums the reaction occurs while the pollen is growing down the style. In the incompatible pollinations the pollen tubes are arrested in the stylar tissue and usually their ends swell up. Roy also found that in certain pollinations which are effective in producing a full crop of fruit, a proportion of the pollen tubes are similarly arrested, indicating at least two pollen genotypes.

In a recent publication (Crane and Brown (3)), it was shown that the varietal and hereditary behaviour of incompatibility in the sweet cherries is determined and governed by a series of multiple allelomorphic genes, the essential feature of which is that pollen cannot function in the style of a plant carrying the same genes as the pollen. At the present stage of our investigations it is not possible to attempt a detailed genetical analysis of the results obtained with plums. It is, however, evident that compared with the discontinuous and comparatively simple behaviour of incompatibility in cherries, in plums not only are the results more complex but fewer groups occur. Also in contrast to the cherries, where in established varieties cross-incompatibility is always reciprocal, in the plums several examples of one-way incompatibility occur.

The plums of the domestica group dealt with in this report have a hexaploid chromosome constitution, $2n=48$, whilst the sweet cherries are diploids, $2n=16$; and there is no doubt that the degrees of incompatibility, reciprocal differences and other complexities found in plums are primarily due to their polyploid constitution. In a polyploid the number of gametic types will be increased and consequently a greater variability in the behaviour of incompatibility, such as its occurrence in degree and in one direction of crossing only, is to be expected. Further, since the nucleus is more complex in plums than in cherries, the chances of individuals of the same constitution meeting to form incompatible groups in plums is lessened.

In these experiments the pollinations are affected by gently rubbing a dehisced anther over the receptive surface of the style. The anther is then left adhering to the sticky surface to show that the flower has been pollinated. That 100 pollen grains are applied to each style would be a reasonable, if not an under estimate. Therefore, in the partially incompatible combinations, such as Blue Rock pollinated with Early Rivers, the Greengages with President or Late Orange, etc., which set only about three fruits out of every 100 flowers pollinated, it follows that only 1 out of 3,000 pollen grains functions. This may be due to a pollen genotype occurring only in such a small proportion. It is, however, more probably the result of a recurring gene mutation, or of a pollen tube representative of a larger genotypic class, as a rarity, travelling the length of the style and bringing about fertilization.

The close resemblances of the fruit characters of the forms of Old Greengage and Cambridge Gage, and the similarity of their incompatibility reactions, suggest that they are all closely related. It is probable that they are seedlings from parents recessive for several major characters, but on the other hand it is possible that they may have originated as bud-sports. Confusion of nomenclature in the Greengages, and the minor nature of their varietal differences, has previously been noted by Bunyard (1) and Dahl (5). Allgrove's Superb originated as a bud sport from Jefferson, and the principal if not the only difference between them is in the colour of their fruits. Crimson Drop and Coe's Violet are both bud-sports from Coe's Golden Drop, and here again the only differences are in fruit colour. The Coe's group, however, is in many ways distinct from Jefferson and Allgrove's Superb.

It is shown in Table II that the average set of fruit obtained from the compatible cross-pollinations is 30 per cent. This approximates to a high yield, but as the individual results detailed in the appended Table VI show, among these compatible crosses considerable variation in the proportion of fruit set occurs. As shown in the paper on cherries (Crane and Brown (3)), the general condition of the trees, whether flowering sparsely or freely, and so on, and other environmental factors, are frequent causes of such differencs. In any case, without repetition and confirmation, it cannot be concluded that lower yields are examples of partial cross-incompatibility. Indeed in plums an analysis of the results and of the interactions of the varieties concerned suggests that these lower yields are in most cases due to environmental causes.

It is evident from the results detailed in the appended Table that the Greengages and the majority of dessert plums have the capacity for very high yields; e.g. Comte d'Althan, the Coe's, Jefferson, Kirke's Blue, Old Greengage, *etc.*, although self-incompatible, have repeatedly carried heavy crops when efficiently pollinated. Therefore, if such kinds are grown in suitable localities and interplanted with varieties with which they are mutually compatible, there is no reason why they should not be consistent bearers and carry heavy crops. As previously pointed out, self-compatible varieties, such as Early Transparent, Denniston's Superb, *etc.*, have so far always proved compatible on self-incompatibles. Consequently as a source of effective pollen, they are valuable kinds to interplant amongst all varieties.

SUMMARY.

In this report the results obtained from self- and cross-pollinations between varieties of the Gage and other dessert plums are described. The results show that they may be classified as follows: (1) self-incompatible, (2) partially self-incompatible, (3) self-compatible varieties.

Table VI.

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Allgrove's Superb.			
Coe's Golden Drop	*154*	*0*	*0*
Coe's Violet	*21*	*0*	*0*
Jefferson	*137*	*0*	*0*
Belle de Louvain	38	29	76
Blaisdon Red	13	8	62
Cambridge Gage	14	8	57
Comte d'Althan's Gage	36	24	66
Denniston's Superb	20	15	75
Diamond	57	8	14
Guthrie's Greengage	39	27	69
Late Orange	42	26	62
Laxton's Gage	32	22	69
Monarch	40	12	30
President	21	9	43
Prince of Wales	32	25	78
Prosperity	39	29	74
Purple Pershore	50	41	82
Rivers' Early Prolific	48	30	62
Transparent Gage	29	19	65
Utility	471	87	18
Victoria	34	28	82
White Magnum Bonum	51	32	63
Blue Rock.			
Rivers' Early Prolific	*737*	*24*	*3*
Allgrove's Superb	17	9	53
Bastard Victoria	52	40	77
Bryanston Gage	28	8	28
Cambridge Gage	63	41	65
Coe's Violet	126	96	76
Comte d'Althan's Gage	130	76	58
Denniston's Superb	80	38	47
Diamond	93	27	29
Goliath	86	38	44
Grand Duke	200	106	53
Guthrie's Greengage	43	13	30
Jefferson	36	23	64
Late Orange	113	70	62
Laxton's Gage	12	4	33
Mallard	157	73	46
Monarch	77	35	45
Old Greengage A.	299	142	45
President	49	39	79
Primate	30	16	53
Prince of Wales	64	51	79
Purple Pershore	105	52	50
Utility	364	163	45
Victoria	180	101	56
Bryanston Gage.			
Cambridge Gage	69	38	55
Early Greengage	42	29	70
Jefferson	460	157	34
Kirke's	41	24	58
Late Orange	62	40	64
McLaughlin's Gage	34	11	32
Old Greengage A.	46	26	56
Old Greengage B.	81	40	49
President	74	19	26
Prune d'Agen	48	17	35
Rivers' Early Prolific	369	59	16
Myrobalan Red	*50*	*10*	*20*
Myrobalan Yellow	*60*	*0*	*0*
Cambridge Gage.			
Late Orange	*733*	*16*	*2*
President	*881*	*14*	*1*
Old Greengage A.	*417*	*8*	*2*
Old Greengage B.	*270*	*2*	*1*
Old Greengage C.	*247*	*4*	*2*
Old Greengage D.	*139*	*1*	*1*
Bastard Victoria	84	30	36
Belle de Louvain	118	47	40
Belle de Septembre	12	5	42
Blaisdon Red	38	10	26
Blue Rock	75	13	17
Bryanston Gage	93	44	47
Coe's Violet	203	109	53
Comte d'Althan's Gage	105	45	47
Czar	105	70	67
Denniston's Superb	52	29	56
Early Favourite	152	112	73
Early Greengage	287	72	25
Early Transparent Gage	136	60	44
Golden Transparent	107	37	35
Grand Duke	41	21	51
Guthrie's Greengage	191	45	24
Jefferson	106	40	38
Kirke's	307	145	47
Laxton's Gage	136	63	46
Mallard	317	56	18
McLaughlin's Gage	33	12	36
Monarch	101	8	8
Oullin's Golden Gage	44	12	27
Pershore	104	62	60
Pond's Seedling	50	16	32
Purple Pershore	371	89	24
Reine Claude de Bavay	134	65	48
Rivers' Early Prolific	63	24	38
Utility	131	39	30
Victoria	188	137	73
Warwickshire Drooper	68	46	68
Coe's Golden Drop.			
Allgrove's Superb	*349*	*1*	*0*
Crimson Drop	*166*	*0*	*0*
Jefferson	*1,112*	*0*	*0*
Belgian Purple	52	11	21
Belle de Louvain	48	24	50
Blaisdon Red	28	6	21
Blue Rock	35	17	48

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Bryanston Gage	343	66	19
Cambridge Gage	57	38	66
Comte d'Althan's Gage ..	125	32	26
Decaisne	42	22	52
Denniston's Superb ..	177	48	27
Diamond	37	7	19
Early Orleans	222	30	13
Early Transparent Gage ..	234	78	33
Golden Transparent ..	314	79	25
Goliath	46	17	37
La Prune Géante	284	38	13
Late Orange..	90	37	41
Late Orleans	353	71	20
Laxton's Gage	71	6	8
McLaughlin's Gage ..	336	77	23
Old Greengage A.	127	49	39
Old Greengage C.	194	37	19
President	54	25	46
Prince of Wales	30	14	46
Primate	95	15	16
Prosperity	188	54	29
Prune d'Agen	175	21	12
Purple Pershore	81	20	25
Transparent Gage	69	21	30
Utility	188	55	29
Victoria	29	9	31
White Magnum Bonum ..	170	38	22
Yellow Magnum Bonum ..	133	39	29
White Damson	70	54	77
Myrobalan Red	*70*	*7*	*10*
Myrobalan Yellow	*84*	*1*	*1*

Coe's Violet.

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Coe's Golden Drop ..	*73*	*0*	*0*
Crimson Drop	*141*	*0*	*0*
Jefferson	*699*	*2*	*0*
Cambridge Gage	71	49	69
Cox's Emperor	187	49	26
Golden Transparent ..	75	4	5
Kirke's	132	56	42
Late Orange..	195	88	45
Late Orleans	78	18	23
Pershore	140	27	19
President	44	31	70
Rivers' Early Prolific ..	157	74	47
Victoria	65	42	65
Frogmore Damson	270	21	8
Prunus spinosa 6x	*347*	*7*	*2*

Comte d'Althan's Gage.

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Allgrove's Superb	51	15	29
Belgian Purple	31	7	23
Belle de Louvain	77	13	17
Blue Rock	16	8	50
Cambridge Gage	136	68	50
Coe's Golden Drop ..	43	5	12
Czar	100	39	39
Decaisne	10	6	60
Denniston's Superb ..	38	5	13
Early Transparent Gage ..	30	19	63
Late Orange..	24	12	50
McLaughlin's Gage ..	69	15	22
Old Greengage A.	140	14	10
Old Greengage C.	81	29	36
Oullin's Golden Gage ..	78	19	24
President	138	22	16
Prince of Wales	53	25	47
Prosperity	45	10	22
Purple Pershore	32	4	12
Rivers' Early Prolific ..	31	12	39
Transparent Gage	21	2	9
Utility	80	21	26
Victoria	210	61	29

Crimson Drop.

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Coe's Golden Drop ..	*87*	*0*	*0*
Coe's Violet	*88*	*0*	*0*
Jefferson	*124*	*1*	*1*
Belle de Louvain	37	13	35
Kirke's	240	51	21
Old Greengage A.	232	73	31
Black Bullace	89	13	15

Denniston's Superb.

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Cambridge Gage	97	31	32
Golden Transparent ..	89	46	52
Jefferson	70	33	47
Old Greengage A.	122	24	21
President	57	28	49

Decaisne.

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Belle de Louvain	63	16	25
Comte d'Althan's Gage ..	75	46	61
Denniston's Superb ..	15	3	20
Jefferson	26	19	73
Late Orange..	64	20	31
Prince of Wales	51	37	72
Purple Pershore	20	9	45
Rivers' Early Prolific ..	176	42	24

Early Greengage.

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Bryanston Gage	96	54	56
Cambridge Gage	111	37	33
Comte d'Althan's Gage ..	117	31	26
Early Transparent Gage ..	73	36	49
Late Orange..	146	31	21
Old Greengage A.	262	20	8
Old Greengage B.	67	10	15
Old Greengage C.	81	54	67
President	162	36	22

Early Transparent Gage.

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Kirke's	119	52	44
Mallard	54	28	52
Pond's Seedling	27	4	15
Prunus Pissardii	*53*	*0*	*0*

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
GOLDEN ESPEREN.			
Allgrove's Superb	68	12	18
Cambridge Gage	60	11	18
Coe's Golden Drop ..	110	14	12
Comte d'Althan's Gage ..	32	4	12
Decaisne	29	5	17
Grand Duke	73	6	8
Jefferson	174	22	13
Late Orange	25	3	12
Laxton's Gage	56	3	5
Mallard	89	5	6
Monarch	223	11	5
Old Greengage A.	119	14	12
Oullin's Golden Gage ..	100	11	11
President	129	16	12
Prosperity	93	8	9
Purple Pershore	67	5	7
Rivers' Early Prolific ..	76	10	13
Utility	28	8	28
Victoria	79	9	11
Kea	98	5	5
GOLDEN TRANSPARENT.			
Cambridge Gage	41	9	22
McLaughlin's Gage ..	71	17	24
President	62	8	13
GUTHRIE'S GREENGAGE.			
Coe's Golden Drop ..	94	28	30
Coe's Violet	14	4	28
JEFFERSON.			
Allgrove's Superb	*272*	*0*	*0*
Coe's Golden Drop ..	*789*	*1*	*0*
Coe's Violet	*431*	*0*	*0*
Crimson Drop	*344*	*0*	*0*
Bastard Victoria	17	14	82
Belle de Louvain	63	24	38
Belle de Septembre ..	43	25	58
Blaisdon Red	171	57	33
Blue Rock	31	25	81
Bryanston Gage	154	92	60
Cambridge Gage	15	11	73
Comte d'Althan's Gage ..	57	31	54
Cox's Emperor	59	45	76
Czar	107	34	32
Decaisne	38	25	66
Denniston's Superb ..	91	50	55
Diamond	79	7	9
Early Greengage	59	42	71
Early Laxton	65	40	61
Early Transparent Gage ..	36	25	69
Gisborne's	105	39	37
Goliath	49	31	63
Grand Duke	203	48	24
La Prune Géante	190	52	27
Late Orange	16	15	94
Late Orleans	429	100	23
Laxton's Gage	128	60	44
Mallard	200	51	25
McLaughlin's Gage ..	64	26	41
Old Greengage A.	130	75	58
Old Greengage D.	55	19	34
Oullin's Golden Gage ..	87	34	39
Pershore	48	18	37
President	53	21	40
Primate	10	3	30
Prince of Wales	28	20	71
Prosperity	30	20	67
Prune d'Agen	234	47	20
Purple Pershore	26	18	69
Reine Claude de Bavay ..	40	27	67
Utility	208	95	46
Victoria	97	83	86
Warwickshire Drooper ..	142	71	50
White Magnum Bonum ..	90	23	25
Black Bullace	24	4	17
Farleigh Damson	164	30	18
Kea	89	34	38
Myrobalan Red	*338*	*18*	*5*
Myrobalan Yellow	*107*	*1*	*1*
Prunus spinosa	*90*	*0*	*0*
KIRKE'S.			
Allgrove's Superb	45	26	58
Cambridge Gage	201	88	44
Coe's Violet	108	25	23
Comte d'Althan's Gage ..	298	59	20
Early Transparent Gage ..	18	7	39
Late Orange	167	66	39
Old Greengage A.	468	117	25
President	124	20	16
Victoria	218	75	34
LATE ORANGE.			
President	*803*	*2*	*0*
Cambridge Gage	314	79	25
Old Greengage B.	146	29	20
Old Greengage C.	63	6	9
Old Greengage D.	87	9	10
Allgrove's Superb	30	6	20
Belle de Louvain	10	4	40
Blue Rock	29	22	76
Bryanston Gage	114	31	27
Coe's Golden Drop	97	36	37
Coe's Violet	94	32	34
Comte d'Althan's Gage ..	33	15	44
Decaisne	77	9	12
Denniston's Superb ..	46	15	33
Early Greengage	116	19	16
Early Laxton	51	8	16
Early Transparent Gage ..	46	13	28
Jefferson	78	19	24
Kirke's	22	6	27
Laxton's Gage	28	12	43

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
McLaughlin's Gage	71	11	15
Monarch	48	11	23
Prince of Wales	29	11	38
Prosperity	10	4	40
Purple Pershore	42	9	21
Reine Claude de Bavay	66	6	9
Rivers' Early Prolific	78	46	59
Transparent Gage	36	7	19
Utility	59	8	13
Victoria	74	34	46
Warwickshire Drooper	112	29	26
White Magnum Bonum	55	18	33
Farleigh Damson	15	6	40
Laxton's Gage.			
Blaisdon Red	79	3	4
Comte d'Althan's Gage	426	45	10
Denniston's Superb	92	19	21
Jefferson	125	11	9
Late Orange	77	13	17
Mallard	36	3	8
Monarch	44	26	59
Old Greengage A.	87	36	41
Oullin's Golden Gage	214	48	22
Utility	246	80	32
Victoria	43	8	19
McLaughlin's Gage.			
Cambridge Gage	37	10	27
Coe's Violet	31	18	58
Cox's Emperor	112	29	26
Early Greengage	71	30	42
Goliath	36	22	61
Jefferson	43	23	43
La Prune Géante	55	11	20
Late Orange	22	7	32
Pond's Seedling	211	58	27
Rivers' Early Prolific	161	73	45
Old Greengage A.			
Late Orange	*169*	*1*	*1*
President	*73*	*0*	*0*
Cambridge Gage	*636*	*5*	*1*
Blue Rock	188	36	19
Bryanston Gage	218	39	18
Coe's Golden Drop	215	39	18
Comte d'Althan's Gage	167	22	13
Czar	207	38	18
Denniston's Superb	110	93	84
Early Greengage	653	132	20
Early Transparent Gage	76	61	80
Jefferson	562	68	12
Kirke's	243	30	12
Laxton's Gage	381	146	38
Oullin's Golden Gage	64	19	30
Rivers' Early Prolific	145	45	31

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Utility	172	85	49
Victoria	94	42	45
Black Bullace	86	18	21
Shepherd's Bullace	42	12	28
Old Greengage B.			
Late Orange	*313*	*4*	*1*
President	*137*	*1*	*1*
Old Greengage A.	*97*	*0*	*0*
Old Greengage C.	*46*	*0*	*0*
Old Greengage D.	*65*	*0*	*0*
Cambridge Gage	*326*	*4*	*1*
Bryanston Gage	172	24	14
Comte d'Althan's Gage	302	32	11
Crimson Drop	444	64	14
Early Greengage	210	17	8
Early Laxton	84	23	27
Mallard	102	31	30
McLaughlin's Gage	217	21	10
Monarch	40	9	22
Reine Claude de Bavay	66	18	27
Warwickshire Drooper	65	27	41
Old Greengage C.			
Late Orange	*36*	*2*	*5*
President	*127*	*6*	*5*
Old Greengage A.	*55*	*2*	*4*
Old Greengage B.	*66*	*0*	*0*
Old Greengage D.	*46*	*1*	*2*
Cambridge Gage	*137*	*2*	*1*
Bryanston Gage	96	30	31
Coe's Golden Drop	21	8	38
Denniston's Superb	88	35	40
Early Greengage	29	11	38
Early Transparent Gage	63	32	51
Kirke's	44	17	39
Old Greengage D.			
Late Orange	*55*	*2*	*4*
President	*85*	*0*	*0*
Old Greengage B.	*71*	*1*	*1*
Old Greengage C.	*125*	*2*	*2*
Cambridge Gage	*137*	*9*	*6*
Bryanston Gage	102	46	45
Coe's Golden Drop	52	15	29
Early Greengage	62	23	37
Victoria	29	16	55
Oullin's Golden Gage.			
Belle de Louvain	48	7	15
Comte d'Althan's Gage	30	15	50
Jefferson	49	27	55
Laxton's Gage	68	22	32
President	106	38	36
Utility	45	23	51
Victoria	48	24	50

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
PRESIDENT.			
Late Orange	*1,151*	*0*	*0*
Cambridge Gage	794	161	20
Old Greengage A.	53	29	54
Old Greengage B.	255	49	19
Old Greengage C.	400	67	17
Old Greengage D.	170	19	11
Belgian Purple	57	13	23
Belle de Louvain	78	20	26
Blue Rock	116	12	10
Bryanston Gage	163	51	31
Coe's Golden Drop	116	60	52
Coe's Violet	74	38	51
Comte d'Althan's Gage	275	76	28
Czar	111	30	27
Decaisne	105	26	25
Denniston's Superb	49	7	14
Early Greengage	144	34	24
Early Transparent Gage	184	69	37
Golden Transparent	61	14	23
Guthrie's Greengage	169	15	9
Jefferson	75	28	37
Laxton's Gage	89	27	30
Mallard	114	33	29
Monarch	201	27	13
Oullin's Golden Gage	40	15	37
Primate	157	76	48
Purple Pershore	40	5	12
Rivers' Early Prolific	18	11	61
Transparent Gage	92	24	26
Utility	100	35	35
Victoria	620	150	24
White Magnum Bonum	196	77	39
Black Bullace	41	26	63
Shepherd's Bullace	19	12	63
REINE CLAUDE DE BAVAY.			
Cambridge Gage	51	12	23
Comte d'Althan's Gage	86	12	14
Early Greengage	123	20	16
McLaughlin's Gage	21	2	9
Old Greengage A.	40	9	22
RIVERS' EARLY PROLIFIC.			
Blue Rock	1,206	334	28
Allgrove's Superb	83	27	32
Belgian Purple	138	31	22
Belle de Louvain	43	32	74
Blaisdon Red	90	10	11
Bryanston Gage	363	110	30
Cambridge Gage	126	57	45
Coe's Golden Drop	187	49	26
Coe's Violet	226	86	38
Comte d'Althan's Gage	98	14	14
Decaisne	195	110	56
Denniston's Superb	75	41	55
Diamond	56	8	14

Pollinations.	Flowers pollinated.	Fruit matured.	Per cent. matured.
Early Favourite	58	36	62
Early Transparent Gage	96	16	17
Gisborne's	346	78	22
Grand Duke	83	14	17
Jefferson	57	23	40
La Prune Géante	270	23	8
Late Orange	273	114	42
Laxton's Gage	88	20	23
Mallard	66	10	15
McLaughlin's Gage	280	28	10
Monarch	162	54	33
Old Greengage A.	178	67	38
Old Greengage C.	184	41	22
Old Greengage D.	88	18	20
Pond's Seedling	88	20	23
President	91	39	43
Primate	211	96	45
Prince of Wales	126	40	32
Prosperity	45	19	42
Purple Pershore	352	64	18
Transparent Gage	184	57	31
Utility	175	93	53
Victoria	50	19	38
White Magnum Bonum	129	46	36
Yellow Magnum Bonum	86	20	23
Prunus coccomillia	*79*	*34*	*43*
TRANSPARENT GAGE.			
Cambridge Gage	171	10	6
Coe's Golden Drop	257	12	5
Comte d'Althan's Gage	151	8	5
Late Orange	136	10	7
McLaughlin's Gage	44	16	36
VICTORIA.			
Bastard Victoria	15	12	80
Cambridge Gage	27	24	89
Coe's Golden Drop	97	34	35
Denniston's Superb	565	241	43
Guthrie's Greengage	45	22	47
Jefferson	107	27	25
Old Greengage A.	162	65	40
Oullin's Golden Gage	112	53	47
Pershore	271	32	12
President	47	27	57
Primate	101	13	13
Prince of Wales	69	11	16
Purple Pershore	144	15	10
Transparent Gage	30	5	17
White Magnum Bonum	199	23	11
Farleigh Damson	15	8	53
King of the Damsons	20	10	50
Merryweather Damson	71	6	8
White Damson	17	12	70
Prunus spinosa	*17*	*0*	*0*
Prunus pissardii	*239*	*22*	*9*
Myrobalan Yellow	*381*	*7*	*2*
Myrobalan Red	*44*	*1*	*2*

Among the wholly and partially self-incompatible varieties cross-incompatibility occurs, both complete and in degree. Sometimes it is reciprocally expressed, but it may occur in one direction of crossing only, the reciprocal pollination yielding a full crop of fruit. In plums the frequency of cross-incompatibility is lower, and its behaviour more complex, than in the sweet cherries. It is concluded that this is attributable to the hexaploid chromosome constitution of the plums.

In the Greengage group varieties occur which are very similar in their morphological characters and also in their incompatibility reactions. It is suggested that they are seedlings from parents recessive for several characters, or possibly that they may have originated as bud-sports.

Degrees of generational sterility occur and are expressed by aborted pollen and imperfectly developed or non-viable seeds.

Since self- and cross-incompatibility are of frequent occurrence in plums, it is necessary to interplant suitable varieties so that provision is made for effective pollination. Varieties in the same incompatible group, and varieties whose flowering times do not coincide, or fail to overlap appreciably, should not be planted together.

REFERENCES.

(1) *Bunyard, E. A.* A Handbook of Fruits. Stone and Bush Fruits. London. 1925.

(2) *Crane, M. B.* Self-sterility and cross-incompatibility in plums and cherries. Journ. Genet., 1925, **15**, 301.

(3) *Crane, M. B.* and *Brown, A. G.* Incompatibility and sterility in the sweet cherry, *Prunus avium* L. Journ. Pom. & Hort. Sci., 1937, **15**, 86.

(4) *Crane, M. B.* and *Lawrence, W. J. C.* Sterility and incompatibility in diploid and polyploid fruits. Journ. Genet., 1931, **24**, 97.

(5) *Dahl, C. G.* Morphological studies of plum flowers. Sverig. Pomol. Fören. Arsskr., 1935, **38**, 131.

(6) *Hooper, C. H.* Plums—notes on their pollination, order of flowering of varieties and insect visitors to the blossoms. Journ. S.E. Agri. Coll., Wye, 1936, **38**, 131.

(7) *Rawes, A. N.* Pollination in orchards, IV. Self-fertility and self-sterility in plums. Journ. Roy. Hort. Soc., 1921, **46**, 353.

(8) *Roy, B.* Studies in pollen tube growth in *Prunus*. Journ. Pom. & Hort. Sci., 1938, **16**, 320.

(*Received* 13/12/38.)

1 Old Greengage "A". 2 Old Greengage "C".

3 Old Greengage "D". 4 Cambridge Gage.

Fig. 1.

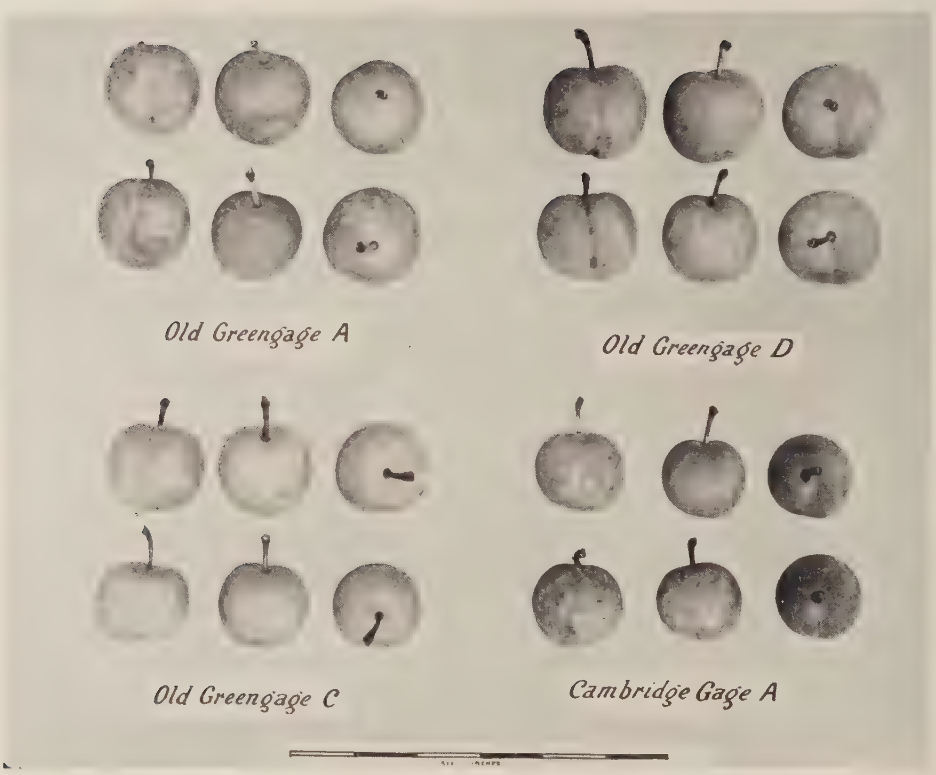


FIG. 2.

Fruits of Old Greengage " A ", " C " and " D " and Cambridge Gage.

Fig. 3.

Old Greengage "D" (Group II) showing compatible and incompatible pollinations. 55 flowers × Bryanston Gage, 34 fruits set; 55 flowers × Late Orange, 2 fruits set; 72 flowers × Old Greengage "C", 0 fruit set; 187 flowers self-pollinated, 0 fruit set.

ROOT STUDIES

VII. A SURVEY OF THE LITERATURE ON ROOT GROWTH, WITH SPECIAL REFERENCE TO HARDY FRUIT PLANTS

By W. S. ROGERS
East Malling Research Station

(a) Introduction.

The important part played by the roots in the life of plants has long been recognized. "The root of the matter", meaning the fundamental cause of any happening, is a common phrase which dates from the book of Job.

The chief functions of roots, anchoring the plant in the soil, absorbing from the soil the bulk of the plant's supply of water and mineral materials, and, in some cases, acting as storage organs, are now well known, and it is generally realized that the reaction of the roots to their environment is a very powerful factor in plant performance (Strasburger (102), Weaver *et al.* (114-117)). There should, therefore, be little need to stress the great importance, in crop cultivation, of a full understanding of plant root habits and the effect of various external factors upon them.

Much careful research has been carried out on the roots of various plants, and the list of references at the end of this paper is only a selection. Nevertheless, knowledge of the growth and habits of the roots of commercial fruit plants under natural conditions is still very incomplete. This is probably because of the difficulty of carrying out researches on large root systems, which are normally so securely hidden in the soil. From his experience, the writer fully supports the statement of Weaver—a tireless and prolific root investigator—that "there is no easy method of studying root systems".

As several writers have reviewed research work on roots, from various aspects, it is not intended to comment here on every paper that is available; but the writer has made a selection of the chief papers on root growth of fruit plants, and of certain other papers of fundamental importance in root growth investigations, from an exhaustive list of over 1,100 titles, kindly supplied by the Imperial Bureau of Horticulture and Plantation Crops, to whom he tenders his grateful thanks. With a few exceptions, when only abstracts were available, the writer has studied all of the papers reviewed, in the original. Many other papers have been excluded on account of the need for brevity.

It is hoped that this survey, which has proved very useful to the present writer and which was primarily designed as a historical introduction to the

next paper of this series, will also be of value to the many new workers now undertaking root investigations.

(b) Previous Reviews of Root Growth Data.

Weaver (114), in his book, "Root Development of Field Crops", gives a historical survey of work in the U.S.A., a general discussion on the functions of roots and the relation of root growth to various soil factors, and a description of the root habits of a large number of native and crop plants, with a bibliography of 232 papers. This book gives a good summary of Weaver's root investigations up to the date of its publication (1926), so they will not be listed here individually. The companion book by Weaver and Bruner (115), "Root Development of Vegetable Crops", also has a bibliography, of 182 papers.

Miller (61) reviewed work on the roots of agricultural plants from 1727 to 1914, and devoted a section to root growth in his book "Plant Physiology" (62), published in 1931, with a list of 205 references bearing on the subject.

Büsgen and Münch, in their book, "The Structure and Life of Forest Trees" (13), have a valuable chapter on root systems. Other notable work on root development of forest trees is that of Laitakari (57) (in Finnish, with an English summary of sixty-two pages), Stevens (100), and Weaver and Kramer (117). Some of the work on forest trees can well be applied to fruit tree problems also; for instance, Stevens (100), in a review of the literature from du Monceau (63) onwards, shows that many workers from the time of Resa (81), in 1877, and including Engler (22), had noted two main periods of tree root growth, one in spring and one in autumn. Stevens' work also showed this, and his conclusions will be discussed later. Lutz, Ely and Little (58) also give a useful review of work on tree roots.

(c) Early Work.

Besides the historic work of Hales (33), dating from 1727, and du Monceau (63), in 1760, attention should also be drawn to the papers of the horticulturist, T. A. Knight (52), in 1806, who described some clever experiments on geotropism of roots and also commented on the absence of persistent tap roots in many trees. In a further paper, (53) in 1811, he showed the tendency of roots to move towards moist soil and noted the more prolific branching of roots in rich than in poor soil. He also considered that tree root thickening was controlled to some extent by the stresses on the trunk.

(d) Fruit Tree Roots in Relation to Soil Profile.

The first worker to make detailed studies on the whole root systems of mature fruit plants appears to have been Goff (30), in 1897, in Wisconsin,

who isolated root systems of apple, strawberry, black raspberry and grape, using the washing out method devised by King (49). A McMahon apple tree, age 7 to 8 years, in a clay loam over sandy clay with sand at 5 ft. had fairly shallow scaffold roots with deep vertical roots descending to 9 ft. No tap root was found in this tree, nor in another transplanted tree 3 years old. In a four-year-old seedling tree that had never been transplanted a tap root was found. In all these plants the roots went far beyond the branch spread. The soil was 12 in. light clay loam over sandy loam.

A year later Goff (31), in 1898, published his findings on root growth in spring, discovered by washing out the soil from trenches in March and April. He found that in many plants, including apple, pear, morello cherry, red currant, white currant and gooseberry, root growth began before shoot growth. The currant was especially early. He also made the following valuable points. (1) Roots grow faster than branches, and hence they spread farther, "as they tend to reduce the plant food in the soil as they proceed they need to extend over a larger area than the stem, to which food is brought by the freely circulating air currents". (2) Root growth in spring is most active near the surface of the soil, which warms up first.

Cranefield (20) investigated the root growth period of apples, pears and plums by digging a trench 2 ft. from the trunk, refilling it, and digging out again in August and October. New roots were found in each case, although twig growth had ceased. Allen (3) reported on apple roots in the Hood River district. He found most feeding roots 3 in. to 10 in. below the soil surface under soil mulch conditions, and deeper in grass mulch.

Ballantyne (6) excavated some fruit tree root systems from a sandy clay soil, underlaid by pure sand, in Utah, under irrigated conditions. He followed only the main roots, which were unearthed by digging a deep trench beside the tree. Jonathan apple, 7 years old, had a root spread of 15½ ft. and a maximum depth of 10 ft. Winter Bartlett pear roots spread over 20 ft. wide and 9 ft. deep, and King Prize peach roots also penetrated to 9½ ft. deep. He suggested that depth is usually about the same as the tree height but that the irrigation method might alter the depth of roots.

McDougall (59) measured root growth in four species of hardwood, and concluded that reduction of root growth in summer is due to water shortage.

Barker (7, 8) studied the root growth of newly planted apple trees at Long Ashton, and concluded that good soil aeration was a very important factor. He also noted some correlation between vigour of individual roots and the individual branches nearly above them.

Peren (79, 80) followed out the horizontal spread of roots of mature trees of cherry, apple, plum and greengage, and noted the very wide root spread. He advocated the wider spreading of manures. He found most roots in the

top 20 in. of soil but followed one root to 77 in. deep. He commented on the severe root competition evidently existing in many orchards.

Burns and Kulkarni (11) excavated roots of five-year-old orange trees and guavas on alluvial loam near Poona. They also found that the roots spread much farther than the branches. They noted the dying back of some roots, apparently due to lack of aeration. Howard (46, 47) reviewed work on the importance of soil aeration, and described his methods for study of roots, at Pusa, India. His main results in root growth appeared later (48), when he described the root penetration of local plum, mango, guava, litchi, lime and loquat, and the effect of grass on tree growth. He washed out sections of the root systems with a knapsack sprayer, and followed local plum roots to a depth of 15 ft. The soil was an alluvial deposit, with blue and yellow clay from 5 ft. to 10 ft. deep, and sandy loam and fine sand below this. He noted the killing of deep roots by a rising water table, and the death of shallow roots in drought periods. The root system grew again in these areas when conditions were favourable again. Thus, in the hot dry weather, only the very deep roots were active, and the small light green leaves at this period suggested nitrogen shortage. He found that grass inhibited the surface roots, except those of the guava, and severely checked tree growth. This effect was attributed mainly to prevention of aeration and reduction of nitrogen supply. The CO_2 in the soil air was markedly increased by grass. Forest trees he found more tolerant of grass. Their deeper roots often followed insect burrows.

A greatly increased interest in the roots of fruit trees was undoubtedly caused by the work of Hatton and his associates, who showed, from 1917 onwards, that the vigour, productivity, fruit quality and many other characteristics of fruit trees could be altered, and to a great extent controlled, by the use of different rootstocks (Hatton (39, 40, 41, 42)).

Hatton, Grubb and Amos (41) also noted the effect of branch pruning and of root removal at the time of planting on root growth of one- and two-year-old apples, showing that severe mutilation of the roots caused reduced growth.

The present writer began studies on the root systems of fruit plants on joining the staff of East Malling Research Station in 1928, and from then to 1932 carried out many detailed excavations. The most important of these was a series of comparable ten- and eleven-year-old apple trees on various rootstocks, ranging from very dwarfing to very vigorous, on loam, sand and clay soils (Rogers and Vyvyan (94)). The great influence of the soil on the position and type of root system was shown. In the poor sand, the main root system was less than 30 cm. deep, and it spread two to three times as far as the branches. Some vertical roots were found, but few descended more than 100 cm. The most vigorous reached a depth of 150 cm. The limiting factor to root depth here was apparently lack of nutrients in the very poor sandy subsoil. In

loam, with the same varieties on the same rootstocks, much better tree growth and a different root conformation was found. The main root system was again fairly shallow, sloping gently downwards and upwards at a depth of 20 cm. to 40 cm., but from this scaffolding numerous vertical roots descended right to the underlying ragstone rock, at a depth of 120 to 300 cm. They then often turned horizontally and ramified profusely in the sticky B horizon soil, just above the rock. Here the depth limiting factor was clearly a mechanical one, the hard rock. The root spread was usually about twice the branch spread, but the effect of root competition between these trees spaced at 15 ft. apart was already noticeable in ten years. The clay, again with the same varieties and rootstocks, showed the influence of yet other factors. The root system was more compact than on loam, but, even so, roots went farther than the branches. The main scaffold roots sloped down to a depth of 50 to 60 cm. and then turned nearly horizontally. No large roots were deeper than 100 cm., a few small ones, of the current year's growth, were found below this, but there were clear signs that such roots had been killed back each year, presumably by a rising water table. Free water was noted at 100 cm. during the excavation, in February. Thus, lack of aeration, due to a shifting water table, was clearly the limiting factor in root depth here. The fact that the main roots were deeper than on loam suggests that summer drying out of the clay surface soil, which cracked badly, may have been the cause. Fine roots grew upwards from the main roots into the top soil, however. This confirms Howard's findings (48).

The different rootstocks covered a wide range of vigour and the roots had very definite and distinct botanical characteristics. The different soils, although modifying the general root conformation, did not change the relative vigour of the rootstocks, or alter the morphological characteristics (such as relative amount of collar fibre, thickness of cortex, colour, fanginess, etc.) of the stocks. Each kept its individuality. Within each soil type, the general root conformation of the different rootstocks excavated was very similar, however. On the loam, for instance, both the most and the least vigorous penetrated to the depth of the rock. It is evident that a dwarfing stock is not necessarily shallow rooted, and the position of the roots, in this investigation, would not explain the stock effects.

The stem : root ratio was also remarkably constant within a soil, whatever the size of tree. Thus, on the sand, it was approximately 1 : 1, while on the loam it was about 2 : 1. This is probably a valid, though rough, measure of the relative fertility of the soils. It also demonstrates the inevitable effect of all root treatments on the branches, and branch treatments on the roots.

The relatively larger root system obtained on poor soil confirms the findings of Aaltonen (1), and Haasis (32), with forest trees.

Another excavation showed the reaction of apple roots to grass and a high water table of moving water on a wet clay soil. Although the root system was restricted, growth was good (Rogers (84)). The great benefit obtained by pears, gooseberries and black currants from the application of farmyard manure to a sandy soil was shown in another study (Rogers (85)). Here, seedling pear and quince roots were found at depths of 337 and 247 cm. respectively, on a sandy loam with a deep water-bearing layer (a different soil from the sand on which the apples grew). The manure, applied to the surface before planting, apparently enabled the roots to grow much more vigorously in the deeper layers as well as near the surface. The stem:root ratio was higher in the manured than in the unmanured trees.

Some excavated apple trees under irrigated conditions were described in a later paper (Rogers (87)), and soil factors were also summarized in a further short paper (Rogers (88)). Beakbane and de Wet (9) also made an interesting excavation study of Bramley's Seedling apple, showing the distinctive root development produced by scion roots; and Hearman (43) made a comprehensive study of the root system of Northern Spy by the East Malling methods. Young pear root systems of compatible and incompatible stock:scion combinations were also excavated at Malling by Chang (17).

Other recent work includes that of Kvarazkhelia (56), who drew a number of interesting conclusions from simple experiments and excavations in Southern Russia, Kurdestan and Georgia (U.S.S.R.). He noted the powerful influence of environment on the roots, especially that of soil aeration, moisture, nutrient content and temperature. Where moisture and nutrients were more abundant, the root system was more compact. He recommended cultivating and manuring over the whole root area, which would be far beyond the branch area. In general, his findings confirm those of the present writer.

Susa (103) also excavated a number of mature apple root systems in Amori, Japan, finding a correlation between root development and soil profile similar to that noted by Rogers and Vyvyan (94), and he recommended cultivation and manuring over the whole orchard rather than in a small circle round the tree.

Kolesnikov (54) noted the sloughing off of the primary cortex and the dying of small apple rootlets in Russia.

Fujimura and Yasuda (29), in Japan, excavated loquats, figs, pears, persimmons, chestnuts, vines and peaches on a sandy soil with high water table, and noted particularly the value of humus in enabling the roots to utilize large soil areas.

Roemer and Hilkenbaumer (82, 83) made rough excavations of a number of twenty-five-year-old apple trees, and noted certain effects of different scion varieties on the root systems, which were mainly of a shallow type.

Vyvyan (111), by digging up and weighing large samples of young apple stocks at intervals over a period of two years, concluded that under some conditions there were two main periods of root growth, and under others, only one.

In the United States of America a wave of interest in root studies produced a number of papers, particularly from 1930 onwards.

Oskamp and his colleagues (69, 70, 71, 72, 73) made a series of studies of root growth of fruit trees in relation to various soil characteristics. He showed that soil areas containing tree roots became more rapidly depleted of moisture than areas not containing roots (69); and that rooting was shallower and tree growth poorer on badly drained than on well drained soils (70). On well drained soils a root depth of 8½ ft. was recorded for mature Baldwin apple. He pointed out that trees whose root systems were restricted by water-logged soils were likely to suffer from drought in dry periods. His root study method was to dig a trench of standard size at a known distance from the tree, and to record the number and size of roots in different positions on the wall of the trench.

Sweet (105) reached conclusions similar to those of Oskamp in relation to deeper root penetration on the better drained soils, using a similar method.

Clark (18) also, by the same method, showed that on a heavy silt loam, at Panhandle, apple and apricot roots were limited to the upper 27 in. of soil.

Partridge and Veatch (76) emphasized the need to take into account the whole soil profile when assessing its value for fruit trees, on account of the many complex factors involved.

Yocum (118) carried out an extensive series of excavations of young Delicious apple trees under various cultural treatments in Nebraska. He found marked responses to varying soil conditions, notably that of soil moisture. Competition from interplanted maize roots caused the apple roots to descend deeply, while a straw mulch conserved moisture near the soil surface and caused a shallow root system. A good review of recent work is given also by this investigator.

(e) BUSH AND SOFT FRUIT.

Relatively little work has been done on bush and soft fruit root systems. In Goff's early studies (30), the roots of three-year-old strawberry plants were found to be mainly in the top 12 in. of soil and to penetrate to a maximum of 2 ft. in light clay over sandy loam. In the black raspberry a shallow scaffolding of roots from which deep roots descended vertically to 5 ft. was found. In a grape, nine years old, very few roots were shallower than 18 in., and roots descended to 8 ft. in a sandy soil below light clay loam.

The root system of the strawberry plant was investigated in a number of careful studies by Ball and Mann (5) and Mann (60) at Long Ashton. These workers found two definite periods of root activity, in spring and autumn, with a slackening of root growth in summer. On their soil, a medium loam, 73% of the roots (by weight) were found in the top 3 in., and 90% in the top 6 in. Only 3% of the roots were more than 13 in. deep.

More detailed study of the root systems of eighteen strawberry varieties was made by Hanson (34), in Colorado, in a heavy clay loam over clay, gradually becoming more sandy as depth increased. Maximum root depth was 40 in., and "working depth" from 8 in. to 30 in. according to variety. The maximum root spread was 6 ft.

Eight-year-old gooseberry and black currant root systems were studied by the present writer, on a deep sandy loam (Rogers (85)). Gooseberry roots penetrated to a depth of over 8 ft., and black currant to 7 ft. Addition of farmyard manure greatly increased the scope of the root system.

(f) Recent Root Studies on Various Other Plants.

Sugar-cane roots have received much attention from investigators. Following the careful studies of root position by Venkatraman (110) and by Roxas and Villano (95), Evans (23, 24, 25, 26, 27, 28) has made a large series of studies, including an attempt to measure the total absorbing surface of the root system. Stevenson and McIntosh (101) have also made some interesting studies on sugar-cane roots in Barbados. Coffee roots have been studied by Sanders and Wakefield (96), Wakefield (112), Trench (106) and Nutman (66, 67), with special reference to cultivation measures. Nutman also tried to measure the total absorbing area. A survey of methods of studying root systems of small plants was made by Pavlychenko (77) and his description of an excellent soil-block-washing apparatus and its application to the study of weed roots should be seen by intending root investigators.

(g) Aeration, Temperature and Other Factors.

Cannon (14, 15) and Cannon and Free (16) made careful studies of aeration and temperature in relation to root growth, and showed the importance of both of these factors. The optimal range for root growth was suggested as being 20° to 31°C. Knight (51) also did some interesting laboratory work on aeration.

Studies on root growth in spray- and water-culture were carried out by Barker (8) and have more recently been developed by Pearse (78) at East Malling; they appear to be particularly useful for nutrient intake measurements.

Harris (35) observed the effect of freezing and submergence in water on apple and filbert root activity in the winter, using field "observation posts",

which cannot quite be called "observation trenches", since the glass had to be removed to make observations. He concluded that "apple and filbert roots, provided they are not submerged, subjected to freezing temperatures or excessive drought, continue growth irrespective of the season of the year". He also studied root activity of young fruit trees, as shown by CO_2-production by the root in special water-culture containers, and showed that injury to the top and exclusion of light both finally resulted in decreased root respiration (36, 37, 38).

Heinecke (44) showed that young apple trees which had all their roots submerged for periods of several weeks while the tree was in full leaf, showed deficiency symptoms in the leaf (presumably because the absorbing rootlets were damaged by lack of oxygen). In 1936 (45), he showed that root growth in two-year-old apples was checked by early defoliation.

Hatton and Amos (41) also showed the importance of leaf action, by demonstrating that root growth was checked by removal of lateral shoots from young trees in summer.

An important study was published by Nightingale (64) showing the effect of various controlled temperatures on root growth of young apple and peach trees, grown in sand cultures. He found practically no root growth at 45° F., maximum root growth at 65°, and rapid suberization at higher temperatures. This agrees very well with the results of the writer's present work.

Otuka (75), in S. Manchuria, also studied the root growth of seedling apple stocks (*Malus baccata* var. Mandshurica) by washing out and weighing at ten day intervals. He concluded that root growth ceased when the soil temperature at 30 cm. deep dropped to about 45° F., and resumed when it reached 32° F. (by which time mean air temperature had been above freezing point for twenty days). He also described (in Japanese) a root observation trench. Watanabe (113), in a study of pineapple root growth, concluded that the minimum root growth temperature was 41° to 45° F., optimum 84° to 88° and maximum 106° to 109°.

Conrad and Veihmeyer (19) showed that soil moisture depletion can, in uniform soil, be used as a measure of root activity below the top 12 in. of soil. Aldrich (2) also deals with moisture usage by roots. This subject has also been closely studied by Rogers (86, 87, 89, 90, 91) using a soil moisture meter developed for the purpose.

Among other papers of interest are those of Noll (65), who mentions exotropy, a property by which lateral roots try to keep as far as possible from their mother-root and from each other, and Von Alten (4), who described two distinct types of young rootlets, which he classified as "feeding roots" and "extension roots".

(h) Root Observation Box Studies.

The old idea of making direct observations on root growth, through glass-walled soil containers, has attracted several workers, since by this method a series of observations can be made on the same roots, without destroying them or removing them from their environment. It is noticeable, however, that few workers have brought their observations to the stage of a full report. Kroemer (55) reported on studies on vine roots growing in concrete containers with a sloping glass wall, observed from a darkened passage lit when required by electricity. He found most active growth in May, June and July, but reported that visible root growth became negligible in the second and subsequent years, and even the original roots disappeared. Dean (21) described two forms of observation box, designed for observation of pineapple roots.

Ostermann (74) used a series of observation boxes for studies on potato root systems. Sideris (99) described a small box with detachable sides, with which certain roots could be isolated and led into glass flasks containing various nutrient solutions.

Schindler (97) used some large root observation boxes for observing apple roots, in grass and clean culture, but the only publication describing results which the writer can trace is a two-page popular article. This shows clearly the checking effect of grass on apple root systems, and also that the grass roots are checked when the grass is cut.

Midway between observation boxes and field observation trenches come the fine root observation chambers of Blaauw (10) at Wageningen. These have been described and used for a number of plants, but, again, full reports seem still to be lacking. Kinman (50), in California, used some simple glass-walled observation trenches and observed the root growth of peach, apricot and Myrobolan plum trees during two seasons, noting two main periods of growth, in spring and autumn, in all cases.

Oppenheimer (68) used root observation chambers at Jerusalem to study oak and pine roots, noting greatest growth from April to June, and a check in midsummer, attributed to drought.

The present writer's observation trenches would appear to be the first in which continuous observations have been described and illustrated, for apples, over more than one season. By means of them, serial photographs and photomicrographs showing the root life history have been obtained. The time, rate and position of growth, suberization, formation of laterals, and secondary thickening or ultimate death were recorded; and the relationship of root growth to soil temperature and moisture was determined. A preliminary report on the methods was published in 1934 (Rogers (86)), and a full discussion of the results obtained over four years, 1933 to 1936, forms the subject of the

following paper of this series. Other studies made with small root observation boxes, which appear very suitable for certain comparative experiments, will be published shortly.

(j) Summary and Conclusions.

A historical survey is made of 118 papers bearing on root growth, with special reference to hardy fruit plants. These papers were selected from over 1,100 works dealing with or mentioning root growth.

General conclusions are that the roots of fruit plants, like those of other plants, owe their characteristics in any given case to the interaction of a number of factors. The first of these, varietal habit, is inborn in the plant, and may persist so that the roots are readily recognizable under a wide range of environmental factors; nevertheless, soil factors control the root system to a large extent. Among the chief soil factors are texture, nutrients, aeration, moisture and temperature. To some degree these can be interdependent. On the whole, the factors first mentioned appear to have the greatest effect on the type of growth, and those mentioned last, on the time of growth; but all these factors must be within certain favourable limits to allow root growth to proceed satisfactorily.

The studies of root habit have all shown that the root system is generally much more extensive than the branch system, and that in trees, and also in many other plants, it may occupy soil layers extending to many feet below the surface. The root will, in fact, grow in any soil area which supplies what it requires, subject to such limiting factors as those listed above. In general, soils that are favourable to deep root development give more vigorous plant growth than soils in which the root range is more restricted.

This survey forms a historical introduction to the following paper in this series, in which the author's observations on growing apple roots (by means of root observation trenches in the field) are discussed, and further discussion on the findings of other workers is presented.

LIST OF REFERENCES.

(1) *Aaltonen, V. T.* Über die Ausbreitung und der Reichtum der Baumwurzeln in den Heidewaldern Lapplands. Acta Forrestalia Fennica, 1920, **14**, 1-55.

(2) *Aldrich, W. W.* Pear root concentration in relation to soil moisture extraction in heavy clay soil. Journ. Agri. Res., 1935, **50**, 975-88.

(3) *Allen, R. M.* Condition of root system of apple trees in the Hood River district. Oregon Agri. Exp. Sta. Rpt., Hood Riv. Br. 1914-15, 1915, 20-4.

(4) *Von Alten, H.* Wurzelstudien. Botanische Zeitung, 1909, **67**, 175-98.

(5) *Ball, E.* and *Mann, C. E. T.* Studies in the root and shoot development of the strawberry. Journ. Pom. & Hort. Sci., 1927, **6**, 87-103.

(6) *Ballantyne, A. B.* Fruit tree root systems: spread and depth as partly determined by excavation on the southern experimental farm, St. George, Utah. Utah Agri. Exp. Sta. Bull. 143, 1916.

(7) *Barker, B. T. P.* Root development in newly planted trees. Long Ashton Res. Sta. Ann. Rpt. 1920, 43-60.

(8) ———. Studies on root development. Long Ashton Res. Sta. Ann. Rpt. 1921, 9-57.

(9) *Beakbane, A. B.* and *de Wet, A. F.* The root systems of some Bramley's Seedling apple trees. East Malling Res. Sta. Ann. Rpt. for 1934 (May 1935), 87-9.

(10) *Blaauw, A. H.* Klein bouwwerk voor Physiologische Cultuurproeven. (With a summary in English. Small building-constructions for physiological cultivation experiments.) Mededeel. Landbouwh, Deel 25, 1923.

(11) *Burns, W.* and *Kulkarni, L. B.* Roots of fruit trees. Agri. Journ. Ind., 1920, **15**, 620-6.

(12) *Büsgen, M.* Einiges über Gestalt und Wachstumsweise der Baumwurzeln. Allgemeine Forst- und Jagd-Zeitung., 1901, **77**, 273-8, 303-9.

(13) ——— and *Münch, E.* Ed. *Thomson, T.* The structure and life of forest trees. Chapman and Hall, London, 1929.

(14) *Cannon, W. A.* Experimental studies on roots. Carnegie Inst. Wash. Yearbook, 1925, **24**, 289-98.

(15) ———. Experimental studies on roots. Carnegie Inst. Yearbook, 1926, **25**, 317-25.

(16) ——— and *Free, E. E.* Physiological features of roots with especial reference to the relation of roots to aeration of the soil. Carnegie Inst. Pub. 368, 1925.

(17) *Chang, W. T.* Studies in incompatibility between stock and scion. Journ. Pom. & Hort. Sci., 1938, **15**, 267-325.

(18) *Clark, E. R.* Root penetration of nine mature fruit trees on heavy silt loam soils. Panhandle Agri. Exp. Bull. 55, 1934, 13-16.

(19) *Conrad, J. P.* and *Veihmeyer, F. J.* Root development and soil moisture. Hilgardia, 1929, **4**, 113-32.

(20) *Cranefield, F.* Duration of the growth period of fruit trees. Wisconsin Sta. Rpt. 1900, 300-8.

(21) *Dean, A. L.* Root observation boxes. Phytopathology, 1929, **19**, 407-12.

(22) *Engler, A.* Untersuchungen über das Wurzelwachstum der Holzarten. Mitt. Schweiz. Zentralanst. forst. Versuchsw., 1903, **7**, 247-317.

(23) *Evans, H.* Studies on root exudation and root types in sugar cane. Mauritius Dept. Agri. Sugar Cane Res. Sta. Bull. 5, 1934, 13.

(24) ———. The root system of the sugar cane. I. Methods of study. Empire Journ. of Exp. Agri., 1935, **3**, 351-62.

(25) ———. II. Some typical root systems. Empire Journ. of Exp. Agri., 1936, **4**, 208-20.

(26) ———. III. The early development of the sugar cane. Empire Journ. of Exp. Agri., 1936, **4**, 325-31.

(27) ———. IV. Absorption and exudation of water and mineral substances. Empire Journ. of Exp. Agri., 1937, **5**, 112-24.

(28) ———. Studies on the absorbing surface of sugar cane root systems. Ann. Bot., Series II, 1938, **5**, 159-82.

(29) *Fujimura, J.* and *Yasuda, R.* Studies on the root systems of fruit trees grown in sandy soil. Journ. Hort. Ass. Japan, 1934, **5**, 69-101.

(30) *Goff, E. S.* Study of roots of certain perennial plants. Wisc. Agri. Exp. Sta. Rpt., 1897, **14**, 286-98.

(31) ———. The resumption of root growth in spring. Wisc. Agri. Exp. Sta. Rpt., 1898, **15**, 220-8.

(32) *Haasis, F. W.* Relations between soil type and root form of western yellow pine seedlings. Ecology, 1921, **2**, 292-303.

(33) *Hales, S.* Vegetable Staticks, 1727, 4-7.

(34) *Hanson, H. C.* Comparison of root and top development in varieties of strawberry. Amer. Journ. Bot., 1931, **18**, 658-73.

(35) *Harris, G. H.* The activity of apple and filbert roots, especially during the winter months. Proc. Amer. Hort. Sci., 1926, **23**, 414-22.

(36) ———. Studies on tree root activities. I. An apparatus for studying root respiration and factors which influence it. Scientific Agriculture, 1929, **9**, 553-65.

(37) ———. Studies on tree root activities. II. Some factors which influence tree root respiration. Scientific Agriculture, 1930, **10**, 564-85.

(38) ———. Studies on tree root activities. III. Scientific Agriculture, 1930, **11**, 191-9.

(39) *Hatton, R. G.* Results of researches on fruit tree stocks at East Malling. Journ. Pom., 1920, **2**, 1-10.

(40) ———. Apple rootstock studies. Effect of layered stocks upon the vigour and cropping of certain scions. Journ. Pom. & Hort. Sci., 1935, **13**, 295-350.

(41) ——— and *Amos, J.* Experiments upon the removal of lateral growth on young apple trees in summer. The effect on stem and root development. Journ. Pom. & Hort. Sci., 1927, **6**, 61-71.

(42) *Hatton, R. G., Grubb, N. H.* and *Amos, J.* Some factors influencing root development. East Malling Res. Sta. Ann. Rpt. for 1923 (1924), 110-19.

(43) *Hearman, J.* Northern Spy as a rootstock. Journ. Pom. & Hort. Sci., 1936, **14**, 246-75.

(44) *Heinecke, A. J.* The effect of submerging the roots of apple trees at different seasons of the year. Proc. Amer. Soc. Hort. Sci., 1933, **29**, 205-7.

(45) ———. Root growth in young apple trees made shortly before and after defoliation. Proc. Amer. Soc. Hort. Sci., 1936, **33**, 164-5.

(46) *Howard, A.* and *G. L. C.* Some methods suitable for the study of root development. Agri. Journ. Ind., 1918, **13** (Sci. Cong. No.), 36-9.

(47) ———. Recent investigations on soil aeration with special reference to agriculture. Agri. Journ. Ind., 1918, **13**, 416-29.

(48) ———. The effect of grass on trees. Proc. Royal Soc. Ser. B., 1925, **97**, 285-317.

(49) *King, F. H.* Natural distribution of roots in field soils. Wisc. Agri. Exp. Sta. Rpt., 1892, 112-20 ; 1893, 160-6.

(50) *Kinman, C. F.* Preliminary report on root growth studies with some orchard trees. Proc. Amer. Soc. Hort. Sci., 1933, **29**, 220-4.

(51) *Knight, R. C.* The response of plants in soil- and water-culture to aeration of the roots. Ann. Bot., 1924, **38**, 305-25.

(52) *Knight, T. A.* On the direction of the radicle and germen during the vegetation of seeds. Trans. Royal Soc., London, 1806. (Also Knight's Horticultural Papers, Longman, London, 1841, 124-30.)

(53) ———. On the causes which influence the direction of the growth of roots. Trans. Royal Soc., London, 1811. (Also Knight's Horticultural Papers, 157-64.)

(54) *Kolesnikov, V. A.* I. The root system of fruit tree seedlings. II. The dying off of rootlets of fruit trees. Journ. Pom. & Hort. Sci., 1930, **8**, 197-203.

(55) *Kroemer, K.* Untersuchen über das Wurzelwachstum des Weinstocks. Landw. Jahrb., 1917, **51**, 673-729.

(56) *Kvarazkhelia, T. K.* On the question of the biology of the root system of fruit trees. (Trans. title) with English summary. Bull. Abkhasian Exp. Sta. Sukhoum 34, 1927. (Also Gartenbauwiss., 1931, **4**, 239-341, with better illustrations.—W.S.R.)

(57) *Laitakari, E.* Mannyn juuristo. Morfologinen tutkimus. The root system of pine (*Pinus sylvestris*). A morphological investigation. Acta Forestalia Fennica, 1929, **33**, 3-380.

(58) *Lutz, H. J., Ely, J. B.* and *Little, S.* The influence of soil profile horizons on root distribution of the white pine. Yale University School of Forestry Bull. 44, 1937.

(59) *McDougall, W. B.* The root growth of forest trees. Amer. Journ. Bot., 1916, **3**, 384-92.

(60) *Mann, C. E. T.* Studies in the root and shoot growth of the strawberry. V. The origin, development and functions of the roots of the cultivated strawberry. Ann. Bot., 1930, **44**, 55-86.

(61) *Miller, E. C.* The root systems of agricultural plants. Journ. Amer. Soc. Agron., 1919, **8**, 129-45.

(62) ———. Plant Physiology, McGraw-Hill Book Co., 1931, 97-149.

(63) *Du Monceau, D.* Des semis et plantation des arbres, et de leur culture. Paris, 1760.

(64) *Nightingale, G. T.* Effects of temperature on growth, anatomy and metabolism of apple and peach roots. Bot. Gaz., 1935, **96**, 581-639.

(65) *Noll, F.* Eine neue Eigenschaft des Wurzelsystems (Exotropy). Bot. Zentralbl., 1895, Jahrg. 15, **60**.

(66) *Nutman, F. J.* Root system of *Coffea arabica*. I and II. Empire Journ. Exp. Agri., 1933, **1**, 271-96.

(67) ———. Root system of *Coffea arabica*. The spatial distribution of the absorbing area of the root. Empire Journ. Exp. Agri., 1934, **2**, 293-302.

(68) *Oppenheimer, H. R.* Études sur le developpement des racines de quelques plantes méditerranéennes. Bulletin de la Silva Méditerranêa, 1935, **10**, 1-23.

(69) *Oskamp, J.* Soil moisture and tree growth relationships. Proc. Amer. Soc. Hort. Sci., 1926, **23**, 269-77.

(70) ———. Rooting habit of deciduous fruits on different soils. Proc. Amer. Soc. Hort. Sci., 1932, **29**, 213-19.

(71) ———. Soils in relation to fruit growing in New York, Part 8. The Tree behaviour on important soil profiles in the Medina-Lyndonville-Carlton area, Orleans County. Cornell Agri. Exp. Sta., Ithaca, N.Y., Bull. 633, 1935.

(72) ——— and *Batjer, L. P.* Soils in relation to fruit growing in New York, Part 2. Size, production and rooting habit of apple trees on different soil types in the Hilton and Morton areas, Monroe County. Cornell Univ. Agri. Exp. Sta. Bull. 550, 1932.

(73) ——— and ———. Soils in relation to fruit growing in New York, Part 3. Some physical and chemical properties of the soils of the Hilton and Morton areas, Monroe County, and their relation to orchard performances. Cornell Univ. Agri. Exp. Sta. Bull. 575, 1933.

(74) *Ostermann, V.* Vergleichende morphologische und physiologische Untersuchungen am Wurzelsystem Verschiedener Kartoffelsorten. Angew. Bot., 1931, **13**, 297-337.

(75) *Otuka, Y.* Studies on the beginning period of the growth and rest period of the apple root. Res. Bull. Agri. Exp. Sta., South Manchuria Railway Co., No. 5, 1931.

(76) *Partridge, N. L.* and *Veatch, J. O.* The relationship between soil profile and root development of fruit trees. Q. Bull. Agri. Exp. Sta., Michigan State Coll., 1932, **14**, 200-7.

(77) *Pavlychenko, T. K.* Soil block washing method in quantitative root study. Canad. Journ. Res., 1937, **15**, 33-57.

(78) *Pearse, H. L.* Apple trees in water culture. East Malling Res. Sta. Ann. Rpt. for 1936 (1937), 131-6.

(79) *Peren, G. S.* Some observations on the extent of root development in mature fruit trees. Long Ashton Res. Sta. Ann. Rpt. for 1921, 21-32.

(80) ———. Data on the lateral spread of the roots of fruit trees. Journ. Pom. & Hort. Sci., 1923, **3**, 96-102.

(81) *Resa, F.* Über die periode der Wurzelbildung. Inaugural dissertation. Bonn., 1877.

(82) *Roemer, T.* and *Hilkenbaumer, F.* Wurzelstudien an 25 Jährigen Kernobstbäumen. Kühn-Archiv., 1936, **42**, 281-303.

(83) ——— and ———. Weitere Beobachtungen über das Wurzelbild 20-jährigen Birnenund Sauerkirschenbusche. Kühn-Archiv., 1937, **44**, 105-20.

(84) *Rogers, W. S.* Root Studies. II. Root development of an apple tree in wet clay soil. Journ. Pom. & Hort. Sci., 1932, **10**, 219-27.

(85) ———. Root Studies. III. Pear, gooseberry and black currant root systems under different soil fertility conditions, with some observations on rootstock and scion effect in pears. Journ. Pom. & Hort. Sci., 1933, **11**, 1-18.

(86) ———. Root Studies. IV. A method of observing root growth in the field ; illustrated by observations in an irrigated apple orchard in British Columbia. East Malling Res. Sta. Ann. Rpt. for 1933 (May 1934), 86-91.

(87) ———. Root Studies. VI. Apple roots under irrigated conditions, with notes on the use of a soil moisture meter. Journ. Pom. & Hort. Sci., 1935, **13**, 190-201.

(88) ———. Soil factors in relation to root growth. Trans. 3rd Internat. Cong. Soil Sci., 1935, **1**, 249-53.

(89) ———. A soil moisture meter depending on the "Capillary Pull" of the soil, with illustrations of its use in fallow land, grass orchards and irrigated orchards. Journ. Agri. Sci., 1935, **25**, 326-43.

(90) ———. The relation of soil moisture to plant growth, illustrated by moisture meter experiments with strawberries. East Malling Res. Sta. Ann. Rpt. for 1935 (May 1936), 111-20.

(91) *Rogers, W. S.* Soil moisture studies. I. Water utilization by apple trees in cultivated and grass orchard compared with fallow land. East Malling Res. Sta. Ann. Rpt. for 1936 (May 1937), 105-9.

(92) ——— and *Srivastava, D. N.* Soil moisture studies. II. Moisture variation in a pear orchard. East Malling Res. Sta. Ann. Rpt. for 1936 (May 1937), 110-13.

(93) ——— and *Vyvyan, M. C.* Root Studies. I. Root systems of some ten-year-old apple trees and their relation to tree performance. East Malling Res. Sta. Ann. Rpt. for 1927, Suppl. II, 31-43.

(94) ——— and ———. Root studies. V. Rootstock and soil effect on apple root systems. Journ. Pom. & Hort. Sci., 1934, **12**, 110-50.

(95) *Roxas, M. L.* and *Villano, M.* Studies on the development of the sugar-cane plant in the Philippines. Root and shoot development of M-1900. The Philippine Journal of Science, 1930, **43**, 367-400.

(96) *Sanders, F. R.* and *Wakefield, A. J.* Further observations on factors in arabica coffee culture. Tanganyika Territory Dept. Agri. pamphlet 8, 27.

(97) *Schindler, O.* Obstbäume und Rasen. Obst-und Gemüsebau, 1931, **77**, 58-60.

(98) *Scott, L. I.* and *Priestley, J. H.* The root as an absorbing organ, I and II. A reconsideration of the entry of water and salts in the absorbing region. New Phytologist, 1928, **27**, 125-73.

(99) *Sideris, C. P.* Container for the study of the behaviour of individual roots. Plant Physiol., 1932, **7**, 173-4.

(100) *Stevens, C. L.* Root growth of white pine. *Pinus Strobus* L. Yale University School of Forestry Bull. 32, 1931.

(101) *Stevenson, G. C.* and *McIntosh, A. E. S.* Investigations into the root development of the sugar cane in Barbados. Brit. W. Indies Cent. Sugar Breeding Ass. Bull. 5, 1935.

(102) *Strasburger, E.* Text-book of Botany. Translated by W. H. Lang. Macmillan & Co., London, 1930.

(103) *Susa, T.* Studies on the distribution of apple roots and methods of cultivation. (Japanese, English summary.) Jap. Min. Agri. Lit. Agri. Improvements, 1934, **81**, 207-28.

(104) *Swarbrick, T.* Factors governing fruit bud formation. VIII. The seasonal elongation growth of apple varieties on some vegetative root-stocks, etc. Journ. Pom. & Hort. Sci., 1929, **7**, 100-29.

(105) *Sweet, A. T.* Soil profile and root penetration as indications of apple production in the lake shore district of western New York. U.S. Agri. Circular 303, 1933.

(106) *Trench, A. D.* Preliminary observations on coffee roots in Kenya. Kenya Dept. Agri. Bull. 2, 1934.

(107) *Ursprung, A.* and *Blum, G.* Zur kenntniss der Saugkraft V. Ber. deut. Bot. Ges., 1921, **39**, 139-48.

(108) *Veihmeyer, F. J.* Some factors affecting the irrigation requirements of deciduous orchards. Hilgardia, 1927, **2**, 125-284.

(109) ——— and *Hendrickson, A. H.* Soil moisture as an indication of root distribution in deciduous orchards. Plant Physiol., 1938, **13**, 169-77.

(110) *Venkatraman, T. S.* Simple contrivances for studying root development in agricultural crops. Agri. Journ. Ind., 1924, **19**, 509-14.

(111) *Vyvyan, M. C.* The distribution of growth between roots, stems and leaves in a young apple tree and its possible bearing on the problem of stock effect on tree vigour. East Malling Res. Sta. Ann. Rpt. for 1933 (1934), 122-31.

(112) *Wakefield, A. S.* Arabica coffee: periods of growth and seasonal measures. Tanganyika Territory Dept. Agri. pamphlet 9, 1933.

(113) *Watanabe, S.* Effect of temperature upon the root development of pineapples. I. Maximum, minimum and optimum temperatures for the elongation of main roots. Communications from Hort. Institute, Taihoku Imp. Univ., No. 24, 1932.

(114) *Weaver, J. E.* Root development of field crops. McGraw-Hill Book Co., New York, 1926.

(115) ——— and *Bruner, W. E.* Root development of vegetable crops. McGraw-Hill Book Co., New York, 1927.

(116) ——— and *Himmel, W. J.* Relation of increased water content and decreased aeration to root development in hydrophytes. Plant Physiol., 1930, **5**, 69-92.

(117) ——— and *Kramer, J.* Root system of *Quercus macrocarpa* in relation to the invasion of the prairie. Bot. Gaz., 1932, **94**, 51-85.

(118) *Yocum, W. W.* Root development of apple trees. Neb. Agri. Bd. Rpt. for 1935, 504-15.

(*Received* 22/12/38.)

ON THE QUANTITIES OF NITROGEN, PHOSPHORIC ACID, POTASH AND LIME REMOVED FROM THE SOIL BY A CROP OF ROSCOFF BROCCOLI DURING ITS GROWTH

By ERNEST VANSTONE and CHARLES E. H. KNAPMAN
Seale Hayne Agricultural College, Newton Abbot

INTRODUCTION.

The quantities of the more important inorganic salts essential to plant growth removed from the soil by ordinary agricultural crops have already been determined in this and other countries. Information on this subject has accumulated in regard to cereal and root crops, but is still lacking for many horticultural crops.

In the West of England, particularly in Cornwall and Devon, the broccoli or winter cauliflower crop is one of great importance. A full account of the cultivation of this crop in that district, including the production of seed, was given by Horne (3) in 1931, whilst Oldham (4), in 1935, published a short review of ten years' work on the broccoli industry in the same area.

Reliable information of the kind indicated above about the broccoli crop and concerning the nutritive value of the mature plant is difficult to obtain, but would obviously be valuable to the grower as a guide to manuring, and to the consumer as affording him useful knowledge as to the nutritive value of this important crop.

According to Stutzer, the dry matter of the crop contains the following:—

Nitrogen ..	4·83 %	Soda	0·549%
Phosphoric acid	1·758 ,,	Magnesia	0·329 ,,
Potash	3·956 ,,	Sulphuric anhydride	1·098 ,,
Lime	0·549 ,,	Silica	0·329 ,,

From these figures it has been calculated that the quantities of inorganic plant requirements extracted from the soil by crops of about 14 and 20 tons per acre, respectively, are approximately:—

Crop.	*Nitrogen.*	*Phosphoric acid.*	*Potash.*	*Lime.*
14 tons.	137 lb.	50 lb.	112 lb.	16 lb.
20 ,,	196 ,,	71 ,,	161 ,,	22 ,,

According to Becker-Dillingen (1, p. 408) a yield of 19·91 tons of broccoli per acre (500 quintals per hectare) removes: Nitrogen 178 lb., phosphoric acid

71 lb., potash 156 lb. and lime 37 lb. It will be seen that the figures for nitrogen and lime differ a good deal from the corresponding ones of Stutzer.

In view of the need for more information concerning the crop as grown in this country the present authors have investigated the following matters:—

(1) The quantities of the essential inorganic requirements of the crop extracted from the soil at various stages of growth, as determined from an experimental plot at the Seale Hayne Agricultural College.

(2) The chemical composition of mature broccoli; the root, stem, leaf and curd being analysed separately.

(3) The chemical composition of broccoli of good marketable quality as compared with that of poor quality ("soft curds").

(4) The chemical composition of broccoli as raised commercially by two well-known growers, in Devon and Cornwall respectively.

EXPERIMENTS AND RESULTS OF 1937.

Sowing, Transplanting, Cultivation and Manuring.

The seed was sown on April 25th, 1937, and planting out was done on June 4th. The plot was ploughed, hand dug and frequently hoed. At planting time, fish manure, at the rate of 5 cwt. per acre, was applied. This supplied 28·78 lb. of nitrogen, 36 lb. of phosphoric acid and 56 lb. of potash per acre. Thus the plot was manured only lightly. There were 12,000 plants per acre, rather more, and therefore closer together, than is usual.

Sampling and Drying.

Samples of the plants were removed at intervals of six weeks, fifty plants being carefully selected to obtain a representative sample on each occasion. In all, eight samples were taken, the first on June 4th, 1937, and the last on March 15th, 1938, nearly eleven months later. After removal to the laboratory the soil was washed from the roots, the leaves were separated and the roots cut up. Roots and leaves were dried separately. In the later stages the stems and the curds were also separated and dried.

For drying, a large square chamber was available, provided with ventilation holes and an electric fan for introducing air. By reversing the fan and using two oil heating stoves the temperature in the chamber could rapidly be raised to 60° C. In this way no great difficulty was found in drying a large mass of material at a low cost. The dry material was ground in an electrically driven mill, thoroughly mixed, and bottled for subsequent analysis. Roots, stems, curds and leaves were all separately treated in similar fashion.

CHEMICAL ANALYSIS.

The material obtained after drying and grinding still contained about 10 per cent. of moisture. Determinations of nitrogen, phosphoric acid, potash, lime, oil and fibre were made, and the results for the first four of these, expressed as lb. removed from the soil per acre, are given in Table I. The results are also shown graphically in Fig. 1.

TABLE I.

Lb. per acre.

		Dry matter.	Nitrogen.	Phosphoric Acid.	Potash.	Lime.
6 weeks	L.	3·84	0·14	0·03	—	0·16
	R.	0·72	0·01	0·003	—	0·02
	T.	**4·56**	**0·15**	**0·033**	—	**0·18**
12 weeks	L.	17·7	0·31	0·12	0·48	0·51
	R.	5·5	0·07	0·04	0·10	0·10
	T.	**23·2**	**0·38**	**0·16**	**0·58**	**0·61**
18 weeks	L.	129	3·93	0·84	5·54	6·26
	R.	30	0·29	0·15	0·78	0·46
	T.	**159**	**4·22**	**0·99**	**6·32**	**6·72**
24 weeks	L.	917	32	8	35	44
	R.	175	2	1	5	1
	T.	**1092**	**34**	**9**	**40**	**45**
30 weeks	L.	1618	51	16	61	63
	R.	413	5	3	11	3
	S.	279	6	3	12	3
	T.	**2310**	**62**	**22**	**84**	**69**
36 weeks	L.	1854	62	19	75	72
	R.	540	7	4	13	4
	S.	393	11	4	18	5
	T.	**2787**	**80**	**27**	**106**	**81**
42 weeks	L.	1721	61	18	76	72
	R.	490	6	4	12	3
	S.	522	14	5	24	7
	C.	51	3	1	2	0
	T.	**2784**	**84**	**28**	**114**	**82**
Mature	L.	1921	63	19	83	98
	R.	714	18	5	17	5
	S.	1082	29	10	46	14
	C.	428	27	8	20	2
	T.	**4145**	**137**	**42**	**166**	**119**

L. Leaves. R. Roots. S. Stems. C. Curds. T. Total.

The percentage composition of the dry matter can be seen from Table II, the results for nitrogen, phosphoric acid, potash and lime being the averages of quadruplicate closely agreeing determinations.

Curve of Growth and Removal of Crop Requirements from Soil.

Up to August 31st, when the rainfall had amounted to 8 inches, growth was very slow, but from September to November it was very rapid, 7·4 inches of rain falling during this period. The rate of growth fell off from November to February, the rainfall during that period being 16·73 inches. In the last period, March and April, there was a rapid increase in the rate of growth, probably associated with the very heavy rainfall during that period and the previous one.

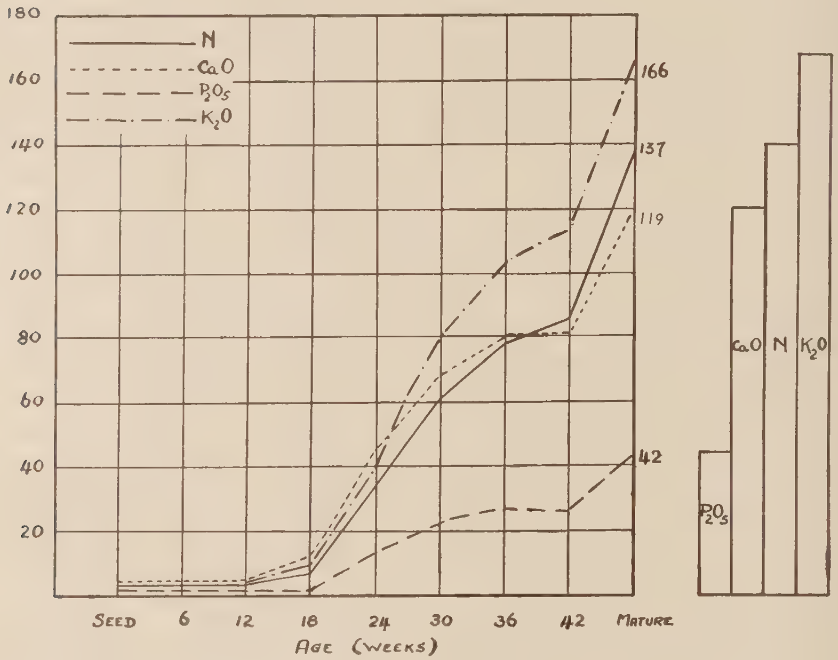


Fig. 1.

Essential inorganic salts removed from soil by Roscoff broccoli during growth (lb. per acre).

From Fig. 1 it will be observed that there was a continuous withdrawal of all four essential inorganic substances, nitrogen, phosphoric acid, potash and lime, from the time of sowing until the crop was cut for the market. Potash was drawn on to the greatest extent—166 lb. per acre. Nitrogen came next—137 lb. per acre. The amount of lime removed was also very large as compared with that withdrawn by the usual farm crops, viz. 119 lb. per acre. Phosphoric acid was removed in least amount—42 lb. per acre.

In Table III the quantities removed by mature broccoli plants are compared

with the requirements of mangolds, turnips and wheat, the figures for the last three being taken from Comber (2, p. 8).

In Table IV the distribution of these materials amongst the roots, stems, leaves and curds of mature broccoli is shown, the percentages being given to the nearest whole number.

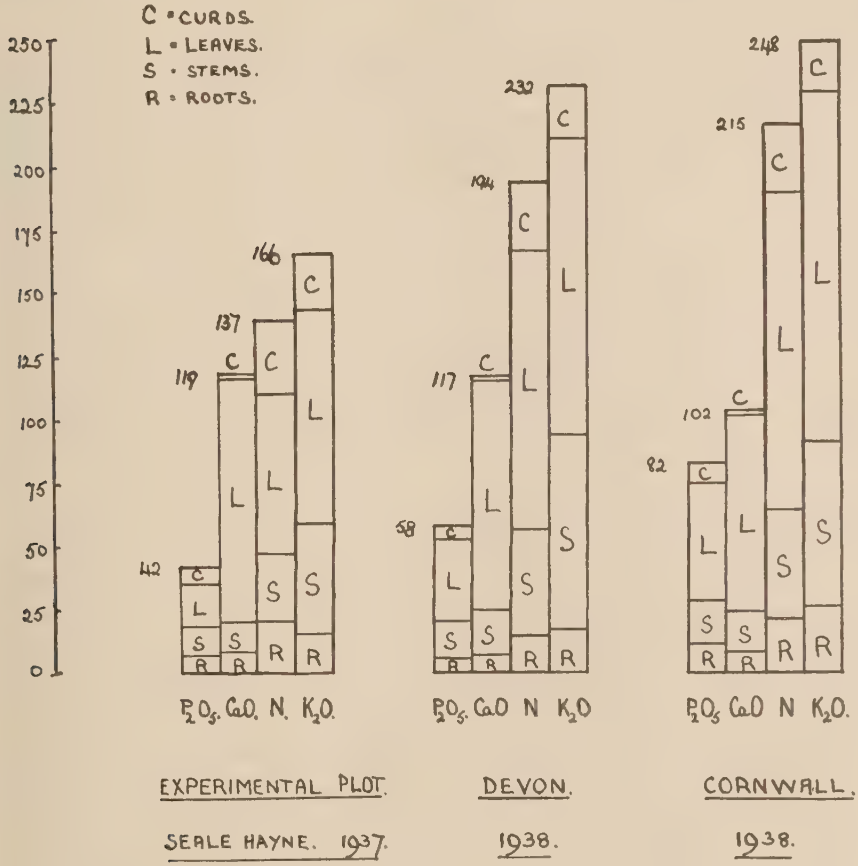


FIG. 2.

Essential inorganic salts removed (lb. per acre).

The figures given in the Tables indicate the great need of the broccoli crop for potash, nitrogen and lime, and the large retention by the leaves of the materials withdrawn from the soil. Of the nitrogen, 46 per cent. remains in the leaves, 21 per cent. in the stems, 20 per cent. in the curd and 13 per cent. in the roots. The phosphoric acid is more evenly distributed, 44 per cent. being found in the leaves, 25 per cent. in the stems, 19 per cent. in the curds and

12 per cent. in the roots. As to lime, the largest amount, 82 per cent., is retained by the leaves, 12 per cent. by the stems, 4 per cent. by the roots and only 1 per cent. by the curds. The figures cannot be regarded as maximum values. They refer to the whole of the plant for a crop of about fourteen tons per acre, grown without farmyard manure and with a comparatively small amount of artificial

TABLE II.

Percentage Composition of the Dry Matter.

		Ash.	Nitrogen.	Protein.	Oil.	Fibre.	N.F.E.	Phosphoric acid.	Potash	Lime.
Seeds		5·05	4·38	27·39	2·62	not	done.	0·38	0·31	0·46
6 weeks	L.	15·64	3·60	22·52	3·24	9·82	48·78	0·79	—	3·97
	R.	10·98	2·00	12·53	2·28	33·18	41·03	0·49	—	2·34
12 weeks	L.	11·48	1·74	10·88	2·24	15·74	59·67	0·69	2·72	2·86
	R.	8·04	1·21	7·55	0·43	49·41	34·57	0·78	1·88	1·90
18 weeks	L.	17·47	3·04	19·00	3·19	13·55	46·79	0·66	4·28	4·83
	R.	7·44	0·95	5·96	0·42	51·50	34·68	0·50	2·55	1·48
24 weeks	L.	16·85	3·47	21·68	2·36	12·66	46·45	0·89	3·84	4·77
	R.	8·07	1·19	7·45	0·54	48·19	35·75	0·60	2·71	0·68
30 weeks	L.	15·20	3·15	19·70	2·63	11·60	50·87	0·96	3·75	3·92
	R.	10·61	1·15	7·16	0·44	44·40	37·39	0·73	2·62	0·71
	S.	10·31	2·17	13·58	0·87	24·21	51·03	0·95	4·36	1·16
36 weeks	L.	15·86	3·32	20·74	2·05	13·68	47·68	1·03	4·07	3·87
	R.	9·31	1·23	7·68	0·36	44·32	38·33	0·78	2·31	0·67
	S.	11·46	2·76	17·27	0·90	22·81	47·57	1·05	4·46	1·24
42 weeks	L.	16·01	3·55	22·17	1·96	12·25	47·61	1·02	4·41	4·16
	R.	8·86	1·26	7·85	0·22	45·79	37·28	0·73	2·35	0·69
	S.	11·67	2·75	17·22	0·48	23·21	47·43	0·97	4·62	1·40
	C.	9·98	6·78	42·37	1·14	11·96	34·56	1·93	4·27	0·64
Mature	L.	17·53	3·28	20·52	2·11	11·82	48·03	0·97	4·30	5·08
	R.	9·11	2·54	15·84	0·16	44·42	30·47	0·71	2·43	0·74
	S.	11·48	2·66	16·65	0·73	19·34	51·81	0·97	4·27	1·29
	C.	12·03	6·33	39·57	1·59	10·29	36·52	1·94	4·64	0·41

L. Leaves. R. Roots. S. Stems. C. Curds. N.F.E. Nitrogen-free extract.

TABLE III.

	Broccoli.	Mangold Roots.	Turnip Roots.	Wheat Grain and Straw.
Nitrogen	137	85	50	60
Phosphoric acid ..	42	50	25	20
Potash	166	250	125	30
Lime	119	25	30	10

fertilizer. A larger crop would, of course, remove proportionately larger quantities from the soil.

COMPARISON OF COMPOSITION OF HARD AND SOFT CURDS.

The chemical composition of broccoli plants of good marketable quality, with hard curds, as compared with that of plants of poor quality, with soft

TABLE IV.

	Nitrogen.	Phosphoric Acid.	Potash.	Lime.
Roots	13	12	10	5
Stems	21	25	28	12
Leaves	46	44	50	82
Curds	20	19	12	1

curds, has been investigated. Messrs. W. P. Mumford & Sons, of Lelant, Cornwall, were good enough to supply twenty-four heads each of good and poor quality. These were separately dried, ground and analysed. Calculated on a basis of 7,000 plants per acre the figures in Table V show the quantities of materials removed from the soil in lb. per acre.

TABLE V.

	Good Heads.				Poor Heads.			
	N.	P_2O_5	K_2O	CaO	N.	P_2O_5	K_2O	CaO
Stem and leaves	32	11	52	24	34	9	37	21
Curds	22	7	19	2	27	7	19	2
Total	54	18	71	26	61	16	56	23

The relative percentage distribution of these materials between stem, leaves and curds is shown in Table VI.

When the percentage composition of the dry matter is considered, it will be seen that there is general agreement between the composition of the plant as grown at Seale Hayne College and in West Cornwall. The percentage chemical

TABLE VI.

	Good Heads.				Poor Heads.			
	N.	P_2O_5	K_2O	CaO	N.	P_2O_5	K_2O	CaO
Stem and leaves	58	63	73	93	56	65	67	92
Curds	42	37	27	7	44	35	33	8

composition of the dry matter in the curds and the leaves + stems at the two places, and of curds in Germany, is shown in Table VII.

The question arises as to why it is that some plants produce dry, firm curds and others soft and watery ones, even when grown on the same soil.

TABLE VII.

	Curds.				Stems and Leaves.			
	N.	P_2O_5	K_2O	CaO	N.	P_2O_5	K_2O	CaO
Seale Hayne ..	6·33	1·94	4·64	0·41	3·28	0·97	4·30	5·08
Cornish, good ..	5·70	1·62	4·69	0·47	3·12	1·07	5·01	2·34
,, inferior	6·41	1·71	4·38	0·43	4·11	1·11	4·44	2·53
German (Stutzer)	4·83	1·76	3·96	0·55	—	—	—	—

Oldham (4) maintains that this is caused by excessive nitrogenous manuring. The analytical results obtained in the present experiments are given in Table VIII.

They confirm Oldham's view that excess of nitrogen tends to soft curds. The outstanding difference is the greater amount of nitrogen in the leaves and curds of the inferior quality plants. The good ones contain less nitrogen in both leaf and curd, and more potash. There is little difference in the total ash content, and there is not much difference in the content of lime and phosphate. The ratio of nitrogen to potash intake would appear to be the most important factor, and the necessity for manurial trials is indicated.

TABLE VIII.

	24 Good Heads.		24 Poor Heads.	
	Leaves.	Curds.	Leaves.	Curds.
Green weight, lb. ..	44·0	17·2	41·0	19·9
Dry weight, lb. ..	3·5	1·4	2·9	1·5
Percentage of water ..	91	92	93	93
	Percentage Composition of the Dry Matter.			
Nitrogen	3·1	5·7	4·1	6·4
Protein	19·4	35·6	25·7	40·1
Ash	13·2	9·6	13·7	9·5
Oil	1·5	1·4	1·7	1·8
Fibre	14·9	12·6	17·7	12·9
N-free extractives ..	50·8	40·8	40·7	35·7
Phosphoric acid ..	1·1	1·6	1·1	1·7
Potash	5·0	4·7	4·4	4·4
Lime	2·3	0·5	2·5	0·4

THE NUTRITIVE VALUE OF BROCCOLI.

(a) *The Curd.* Since this is the part of the plant preferred as a vegetable it will be of interest to consider its food value as compared with that of dried milk. The chemical composition of these two foods is as follows:—

	Broccoli Curd.	*Dried Milk.*
Protein	39·56%	27·30%
Oil	1·58 ,,	29·34 ,,
Fibre	10·30 ,,	—
Ash	12·03 ,,	5·86 ,,
N-free extractives* ..	36·53 ,,	37·50 ,,

The curd is evidently a highly nutritious food, rich in protein and mineral matter, but deficient in fat. The method of serving this vegetable with butter, however, compensates for the lack of fat in it, and in this way makes it practically a perfectly balanced food. It is also worthy of note that the mineral matter is particularly rich in phosphoric acid, and that since most of the lime remains in the leaves, the curd must contain organic phosphorus compounds analagous to the casein of milk. Although the vitamin content has not been investigated, it can surely be stated that such a fresh vegetable will not lack vitamins. Broccoli, therefore, stands out as a vegetable of the greatest value for food and health. It has been shown that even after cooking, the dry matter contains 38 per cent. of protein (5).

(b) *The Leaves.* In packing for transport and marketing most of the leaves are removed. Growers have long known that the leaves have a high feeding value and they are considered valuable by dairy farmers in their rations for milk production.

The chemical analysis of the dry matter of the leaves is shown below and, for comparison, that of palm kernel cake (extracted), aftermath and young grass.

	Broccoli Leaves.	*Palm Kernel Cake.*	*Aftermath.*	*Young Grass.*
Protein	20·51%	21·11%	20·78%	21·22%
Oil	2·11 ,,	2·22 ,,	5·44 ,,	5·67 ,,
Fibre	11·82 ,,	17·77 ,,	20·46 ,,	17·68 ,,
Ash	17·52 ,,	4·44 ,,	7·77 ,,	8·98 ,,
N-free extractives ..	48·04 ,,	54·46 ,,	45·54 ,,	46·45 ,,

From the above comparative figures it can be seen that the chemical composition of broccoli leaves closely resembles that of palm kernel cake with low oil content and that of the aftermath of hay plots in July, after cutting in June, and of young grass. The leaves are superior since they possess much less fibre and have a much larger quantity of mineral matter. It has already been

* Mainly carbohydrates.

pointed out (Table IV) that 82 per cent. of the lime taken up from the soil remains in the leaves, and it will be seen from Table II that for broccoli grown at Seale Hayne College, more than 5 per cent. of the dry matter consisted of lime. When it is realized that most farm crops and purchased foods are deficient in this mineral substance, and that lime is of great value for bone formation, milk production and the general well-being of stock, the value of broccoli leaves as a food becomes specially significant.

It would appear that the use of commercial driers for drying the waste parts of vegetables may be as important as for grass. In a paper on grass drying, Woodman (6) states that, on the basis of dry matter, after mid-May, monthly mown grass contains 13 per cent. of digestible protein and 66·5 per cent. of starch equivalent. Thirty pounds of dried grass with 13 per cent. of digestible protein supplies enough for a 5-gallon cow, and would contain sufficient lime and phosphoric acid. Assuming that 80 per cent. of the constituents of broccoli leaves are digestible, the starch equivalent would be :—

Digestible protein ..	15·4	
Oil	3·8	67·2.
Carbohydrates and fibre	48·0	

They would thus appear to be superior to young grass, since they contain the same starch equivalent but a higher protein content, less fibre and more mineral matter, including lime.

EXPERIMENTS AND RESULTS OF 1938.

The broccoli grown on the experimental plot at Seale Hayne College in 1937 received but little fertilizer, and the plants were comparatively small. Those received from West Cornwall were mainly heads, with little leaf or stem. It was therefore decided to investigate the composition of broccoli produced in 1938 by two representative growers, one from Devon and one from Cornwall. In this way it was possible to study differences in chemical composition when soil, climate, season and manuring were different.

Twenty-five whole broccoli plants with leaves and roots were collected from the farm of Mr. L. E. Ashford, Lower Netherton, Newton Abbot, Devon, on March 3rd, 1938, and a similar number from that of Messrs. Mumford & Sons, Polgrean, Hayle, Cornwall, on March 9th. On each of these farms the mature plants were very large and of excellent quality. They were grown 2 ft. 6 in. apart and the same distance between the rows, so that there were approximately 7,000 plants per acre.

The Devon broccoli were grown on land that had previously been down to grass for three years. They received 6 cwt. of sulphate of potash and 4 cwt. of superphosphate per acre. In addition, one half of the field was given 10 tons

of farmyard manure, but it was the opinion of the grower that this could have been omitted without disadvantage.

The Cornish broccoli were grown on light land which had received 15 tons of farmyard manure and poultry manure together with 7 cwt. of a mixed fertilizer containing 12 per cent. soluble phosphoric acid, 3·5 per cent. citric-soluble phosphoric acid, 2 per cent. insoluble phosphoric acid, 3·69 per cent. nitrogen and 6 per cent. potash. A comparison of the manure supplied in lb. per acre is given in Table IX.

The treatment in Devon was much more liberal in potash and nitrogen, and that in Cornwall provided an excess of phosphoric acid. This is reflected in the yield of dry matter, the total per acre from Devon being 2·5344 tons and that from Cornwall 2·2678 tons.

Full details of the yields and the analyses made are given in Tables X, XI and XII.

TABLE IX.

	Devon.	Cornwall.
	lb. per acre.	lb. per acre.
Potash	323	47
Phosphoric acid	72	Soluble 94; Citric soluble 27; Insoluble 16 } 137
Nitrogen	from 10 tons F.Y.M. from grassland	from 15 tons F.Y.M. from meat and bone meal 29

TABLE X.

Yield of Dry Matter in tons per acre.

	Curds.	Leaves.	Stems.	Roots.	Total.
Devon	0·18	1·27	0·65	0·43	2·53
Cornwall	0·17	1·21	0·54	0·34	2·26

TABLE XI.

Percentage Composition of Dry Matter.

	Devon.				Cornwall.			
	Curds.	Leaves.	Stems.	Roots.	Curds.	Leaves.	Stems.	Roots.
Nitrogen ..	6·88	3·81	2·75	1·82	6·96	4·61	3·71	2·37
Protein ..	43·02	23·82	17·19	11·34	43·51	28·72	23·16	14·79
Ash	9·52	15·33	12·24	7·36	10·37	15·32	12·23	8·92
Lime	0·41	3·12	1·38	0·66	0·36	2·95	1·14	0·91
P_2O_5	1·72	1·06	0·95	0·67	2·03	1·62	1·59	1·47
K_2O	4·78	4·26	4·78	2·25	5·27	5·10	5·55	3·03

TABLE XII.

Materials Removed in lb. per acre.

	Devon.					Cornwall.				
	Curds.	Leaves.	Stems.	Roots.	Total.	Curds.	Leaves.	Stems.	Roots.	Total.
Nitrogen	28	108	40	18	**194**	27	125	45	18	**215**
Protein	178	678	250	110	**1216**	167	782	283	113	**1345**
Ash ..	39	436	178	71	**724**	40	416	149	68	**673**
Lime ..	2	89	20	6	**117**	1	80	14	7	**102**
P_2O_5 ..	7	30	14	7	**58**	8	44	19	11	**82**
K_2O ..	20	121	69	22	**232**	20	138	67	23	**248**

Although the heavier manuring of the Devon crop produced one quarter of a ton more dry matter, this had a lower percentage of nitrogen, phosphoric acid and potash in every part of the plant, but a slightly higher percentage of lime, than that of the Cornish crop. The removal of essential inorganic materials by these crops was much greater than that by the experimental crop at Seale Hayne College in the previous year.

Great demands are made by the broccoli crop on nitrogen and potash. The amount of nitrogen removed per acre is equivalent to that which would be contained in half-a-ton of sulphate of ammonia, and that of potash to that contained in 5 cwt. of sulphate of potash (48 per cent.). This, however, does not mean that the nitrogen should be supplied in the form of sulphate of ammonia, for experience has proved that the nitrogen supply should be available slowly. Hence one grower supplied it by ploughing up a temporary ley whilst the other gave it in the form of farmyard and poultry manure together with meat and bone meal.

It will be observed that there is a general similarity in the composition of the plant independent of the location of the crop or its manurial treatment. The percentage composition of the broccoli grown at Seale Hayne College agrees fairly closely with that of the crop grown a few miles away at Lower Netherton on a different kind of soil. The composition of the Cornish broccoli also does not differ very markedly from that of the others. The similarity applies not only to the plant as a whole but also to the separate parts, curds resembling curds, and leaves, leaves, in chemical composition. To some extent this would be expected, since the variety grown in Cornwall and at Seale Hayne College was the same.

Attention is drawn to the comparatively large intake of lime. Few agricultural crops make so large a demand as this, hence growers should see that their land for broccoli crops receives adequate supplies. On the other hand, the amount of phosphoric acid removed is comparatively small. The Cornish crop was particularly well supplied with this compound, and this is reflected to a

remarkable extent in the composition of the various parts of the plant. Each part of the Cornish broccoli has a higher percentage of phosphoric acid than the corresponding part of the Devon plant, and 82 lb. were removed per acre by the Cornish as compared with 58 lb. by the Devon crop.

The figures obtained cover crops grown in two seasons, 1937 and 1938, and on three types of soil ; nevertheless there is no very great variation in chemical composition. This can be seen from the composition of the curds given in Table XIII.

Table XIII.

Comparative Chemical Composition of the Curds.

		N.	P_2O_5	K_2O	CaO
Seale Hayne College	1937	6·33	1·94	4·64	0·41
Cornwall	1937 Good	5·70	1·62	4·69	0·47
Cornwall	1937 Bad	6·41	1·71	4·38	0·43
Newton Abbot	1938	6·88	1·72	4·78	0·41
Cornwall	1938	6·96	2·03	5·27	0·36

Whilst this crop is grown mainly for human consumption of the head or curd, it should be noted that the main yield consists of leaves. Half of the dry matter of the plant consists of leaves. As much as 6 cwt. of protein (albuminoids) were produced by the Devon grower, and 7 cwt. by the Cornish one. This should be fed to produce milk or meat rather than be returned to the soil direct as manure. It should prove an excellent feed for stock.

The results obtained so far in the present work point to the need for a thorough investigation of the best method of supplying the requirements of the crop and to the need for scientifically designed field trials to determine the effect of fertilizers on yield and quality. For a reduction of the ratio of leaf to curd, plant breeders must be called in to help. The present work has shown that for every 1 lb. of curd, 7 lb. of leaves are produced.

SUMMARY.

(1) The chemical composition of Roscoff broccoli plants at various stages of their growth on an experimental plot in Devon has been investigated ; stem, leaves and curds being analysed separately.

(2) Sown in April and transplanted in June, growth was most rapid during September, October and November. Maturity was reached in April of the following year.

(3) Materials were removed from the soil continuously during the whole period and the rates of such removal are given.

(4) The dry matter of the curd contains no less than 40 per cent. of protein, and the nutritive value of the curd is compared with that of dried milk.

(5) The dry matter of the leaves contains over 20 per cent. of protein, and they should therefore prove of great value as food for stock. It is compared with that of palm kernel cake and young grass, which it closely resembles.

(6) It is shown that good quality curds differ from those of inferior quality ("soft curds") by having a higher percentage of potash and a lower percentage of nitrogen than the latter.

(7) The chemical composition of Roscoff broccoli and the amounts of nitrogen, phosphoric acid, potash and lime removed from the soil per acre, were determined for this crop when grown:—

(a) on an experimental plot at Seale Hayne College in 1937;
(b) on well manured land in Devon in 1938;
(c) on lighter land in Cornwall in 1938.

The results showed that there was a general similarity in the composition of the plant independent of location and manuring.

(8) The average amounts of essential inorganic materials removed by the crop from the soil per acre were found to be: Nitrogen, 204 lb.; phosphoric acid, 70 lb.; potash, 240 lb.; lime, 110 lb.

ACKNOWLEDGMENTS.

The authors desire to acknowledge the ready co-operation of Messrs. Mumford & Sons, of Polgrean, Hayle, Cornwall, and of Mr. L. E. Ashford, of Lower Netherton, Newton Abbot, Devon, as well as of Mr. F. R. Horne and other members of the Seale Hayne College Staff. They also wish to thank the Fertilizer Manufacturers' Association, Ltd., and Dr. P. Krische, of the Deutsche Kalisyndikat, Berlin, for information they have so willingly given.

REFERENCES.

(1) *Becker-Dillingen, J.* Handbuch der Ernährung der gärtnerischen Kulturpflanzen. Berlin, 1933.

(2) *Comber, J.* Introduction to the Scientific Study of the Soil. London, 1936.

(3) *Horne, F. R.* The Life-history of Broccoli. Journ. Min. Agric., 1930/31, **37**, 1100.

(4) *Oldham, C. H.* The Broccoli Industry. Journ. Min. Agric., 1934/35, **41**, 1063.

(5) Special Report of the Privy Council Medical Research Council, No. 213, 1936.

(6) *Woodman, H. E.* The Artificial Drying of Young Grass. Journ. Min. Agric., 1934/35, **41**, 1050.

(*Received* 12/10/38.)

ROOT STUDIES

VIII. APPLE ROOT GROWTH IN RELATION TO ROOTSTOCK, SOIL, SEASONAL AND CLIMATIC FACTORS*

By W. S. ROGERS
East Malling Research Station

I. METHODS.

A HISTORICAL review of research work bearing on root growth of fruit plants, which forms paper No. VII of this series of studies (Rogers (14)), showed that a fair amount of information had been obtained on the distribution of roots in the soil under various conditions, but that relatively little was known about the actual absorbing roots. Such roots, being small and succulent, are generally lost in root excavation methods, and, in any case, by these methods the entire root system is destroyed, making further records on growth or behaviour unobtainable.

Various types of root observation box provided with glass panels held against the soil, dating from the time of Sachs, have been tried by several workers, since by this method observations can be made on the young roots without destroying them ; but technical difficulties appear to have severely limited work on these lines. A review of this work also is given in the paper quoted above.

The method appeared promising, however, and it was therefore decided to try to obtain further information on the growing and absorbing roots of a fruit tree by the use of root observation trenches of a new design, which, it was hoped, would make possible a continuous series of observations under orchard conditions over a period of several years. It was thus proposed to obtain information on the time, position and rate of root growth, and on the way in which the roots respond to changes of soil conditions.

Accordingly four observation trenches, designed by the writer, were installed in an apple orchard at East Malling ; and the present study consists of observations made in them. Special work concerning the development of a soil moisture meter in connection with this study has been published separately (Rogers (11, 12, 13)).

* The present paper is part of a Thesis approved for the Degree of Doctor of Philosophy in the University of London.

(a) Construction of the Observation Trenches.

The trenches (Series D) consist of wooden cabins sunk in the ground, housing vertical windows of $\frac{1}{4}$ in. plate glass, held against the soil in a strong steel framework, at a distance of about 2 ft. 6 in. from the trunk of the tree, and placed tangentially to a circle of which the tree trunk is the centre, as shown in Fig. 1, Plate I. The vertical (or nearly vertical) position of the windows is probably the main secret of success, as this overcomes the tendency, so marked when the glass slopes under the soil, for the finer soil particles to accumulate against the glass and so to obscure the root growth. It also makes observation and recording of the behaviour of the roots much easier. The problem of keeping the glass in good contact with the soil is overcome by the use of a spring mounting.

The cabin is about 7 ft. 6 in. long, 4 ft. wide and 4 ft. 6 in. deep, and has steps at one end. The roof is hinged and the joints are fitted with light-traps. The glass area is 3 ft. 8 in. high and 2 ft. 8 in. wide, divided into six main sections, each with a light-proof wooden shutter.* When fitting the window, the soil which is to come next to the glass is removed in layers, air-dried and re-packed against the glass in its original layers. This is essential to produce an accurate profile in good contact with the glass.

Each window was marked with $\frac{1}{2}$ in. squares, whose rows and columns were lettered and numbered for reference. The glass used in Series D was "Pilkington's wired Georgian Plate", which contains steel wires forming $\frac{1}{2}$ in. squares. In other cases, $\frac{1}{2}$ in. squares were ruled with a writing diamond. The inside face should be ruled before installation to avoid parallax. This marking in squares is important as it enables each new root to be charted accurately on a plan.

All the windows faced north, so that direct sunlight never fell on the roots, and observations were made by daylight, in as short a period as possible.

Fuller details of the installation have been given in a preliminary paper (Rogers (10)) which also discusses the advantages and drawbacks of the method. Most of the points there made, e.g. the advantage of continuous records on the same roots, the near approach to field conditions, the limitations of the relatively small samples visible, and the drawback of exposure of the roots to light, are well demonstrated in the present studies. The last point has been dealt with fully in a separate study, which forms the subject of a further paper in this series (see p. 131). One objection often raised, viz. that it is unnatural for a root to grow in contact with glass, is not so serious as might be thought, for a pane of glass is really like a large smooth flint or a grain of sand.

* Working drawings and detailed carpenters' and engineers' specifications are available to any workers interested.

(b) EXPERIMENTAL MATERIAL.

Three trenches, as described above, were installed in the spring of 1932, against fourteen-year-old Lane's Prince Albert apple trees. Two of the trees were on the very dwarfing rootstock, Malling No. IX, and one on the very vigorous rootstock, No. XVI. A fourth trench, on similar lines but of rather different dimensions (Series C), shown in Fig. 2, Plate II, had been installed in the same plantation against a sister tree on No. I rootstock in the spring of 1931. These four trenches, therefore, cover the range of rootstocks from very dwarfing to very vigorous. The trees formed part of a rootstock trial, and detailed records of their vigour and cropping had been taken since the time they were planted. Tree size data are given in Table I, which shows the typical contrast in vigour and cropping of the different stocks.

TABLE I.

Tree Size and Crop Data.

Lane's Prince Albert Apple, age in 1932, 14 years.

Observation Trench	C1.	D1.	D2.	D3.
Date installed (spring)	1931	1932	1932	1932
Stock	I	IX	IX	XVI
Tree Height, m., March, 1931 ..	2·6	2·4	2·0	3·5
Mean Spread, m., 1931	4·3	3·5	3·3	5·3
Trunk girth, cm., May, 1932 ..	37·6	27·4	24·1	47·3
Crop, lb. 1933	102·6	95·7	74·0	91·0
1934	73·5	105·9	92·2	212·8
1935	2·0*	0·3*	1·1*	0·4*
1936	149·5	105·6	91·3	231·7

* Frost destroyed blossom.

(c) SOIL.

The soil was a fertile sandy loam. The top soil was dark in colour, and 20 to 30 cm. deep ; the subsoil was lighter in colour, of compact sandy loam, extending to a depth of 90 to 120 cm. A marked B horizon occurred below this, of dark, chocolate-coloured, sandy clay, locally known as "Pug", containing many minute air channels. This layer varied in thickness from about 5 to 15 cm., and below it came the Ragstone rock of the Hythe beds geological formation. The Ragstone is a calcareous sandstone rock, grey to yellow in colour. It occurs in alternate layers with similar uncemented material called "Hassock", and forms a very free draining base to the soil. The B horizon is usually very moist, however. This soil profile is typical of the Malling series of the Kent Fruit Soils Survey. An analysis of the different layers, kindly carried out by Dr. Goodwin of Wye College, gave the results shown in Table II.

(d) RECORDS OBTAINED IN THE OBSERVATION TRENCHES.

A few weeks after installation of a trench a number of apple roots could be seen growing against the glass. By periodical removal of the shutters the roots could be inspected, and the time, amount and position of new root growth could be recorded. The suberization of the root and its subsequent performance could also be recorded. The root hairs could be watched through a microscope, and photomicrographs could be taken, as well as ordinary photographs. Records of the condition of the roots were usually made weekly, but records of those growing against certain windows in each trench were made monthly.

TABLE II.

Analysis of Malling Series Soil Profile.

Depth.	0–17 cm.	17-33 cm.	33-50 cm.	50-100 cm.	"Pug"	"Hassock"
On Air-dry Sample						
Moisture	2·55	2·11	2·35	3·05	7·26	2·59
Loss on Ignition ..	4·20	1·92	2·22	2·46	4·89	0·00
$CaCO_3$	0·11	2·03	0·03	0·05	0·26	7·30
Loss by Solution ..	1·68	2·72	1·06	1·05	2·49	5·16
Coarse Sand ..	32·52	31·70	29·52	48·77	26·55	61·73
Fine Sand ..	21·99	22·94	23·28	16·50	11·90	7·00
Silt	17·55	16·68	19·20	8·10	4·65	4·10
Fine Silt	7·20	7·62	7·80	5·70	8·60	1·85
Clay	11·60	12·00	14·00	14·00	33·60	10·60
	99·40	99·72	99·46	99·68	100·20	100·33
Total Nitrogen ..	0·159	0·081	0·068	0·032	0·038	0·018
Total P_2O_5 ..	0·300	0·225	0·213	0·000	0·182	0·189
Total K_2O	0·185	0·214	0·252	0·357	1·289	1·150

Each new root was drawn on a full-sized plan, marked with squares corresponding to those on the windows. When there was little growth, the drawing was made with an ordinary H pencil, and the date was written beside each root. In the periods of greatest growth, coloured pencils were used—a different colour for each week. This saved much time and was very helpful, since at the peak periods of growth the actual drawing of the roots (sometimes amounting to hundreds on a single window) took several hours. From 1932 onwards, the length of each new root, its position and its total unsuberized length was entered on a record sheet at the time the roots were drawn. This made summarizing easier, and also gave greater accuracy in drawing the roots from week to week, since full particulars of the previous week's growth could be seen at a glance. The time of removal and replacement of each shutter was also noted so that the length of time of exposure to light of each batch of roots was known. Two trials, described in a later paper (see p. 131), showed that exposure to light checks root growth, but not sufficiently to vitiate the results.

A box-like wooden stool, providing alternative seat-heights of 16 in. and 8 in., proved very helpful when making observations, as it enabled the eye to be brought near to the root level.

Further factors that were recorded were soil temperature at various depths, rainfall, and, from 1932 onward, soil moisture. The last-named record was obtained with the soil moisture meter devised by the writer and already mentioned. This instrument gives a direct and continuous measurement of the "suction force" of the soil, or "soil moisture tension", which varies with the particle size, degree of packing and moisture content of the soil. The first two factors remain constant for one position, hence variations in soil moisture tension give a measure of the soil moisture variations. This will be discussed more fully later.

Shoot growth records were obtained by weekly measurement of ten marked shoots on each tree, and notes were made on the condition of the tree as regards blossom, leaves, fruit, etc.

(e) PHOTOGRAPHIC METHODS.

A large number of photographs were taken and it was found that this was the best method for recording certain points. The poor lighting conditions and the liability to reflections on the glass surface presented difficulties, but the bad effect of reflections was usually overcome by holding a black cloth behind the camera. In some cases it was necessary to place a black cloth over the camera front itself, with a hole cut for the lens. Photomicrography made possible the obtaining of some very interesting series of pictures and the arrangement that proved most successful is shown in Fig. 2, Plate II. A triple extension camera is clamped to a rigid wooden bracket, which can be screwed to the trench framework in the desired position. A special photomicrographic microscope objective (equipped with a diaphragm) is held in the lens panel, and, with an available bellows extension of 21 in., magnifications of about 7·0 with a 3 in. objective, 10·5 with a 2 in. objective, and 21·0 with a 1 in. objective are obtained. The last-named is rather difficult to use in the trench, but 3 in. and 2 in. objectives proved very satisfactory. The amount of light projected on to the focusing screen is so small that a completely light-proof focusing sleeve attached to the camera with elastic is necessary to allow sharp focusing. A rising and sliding front on the camera is a great help for the final locating of the object.

The wires embedded in the plate glass in the Series D trenches, though helpful in marking the position of roots, are rather a drawback in photomicrographs, for they hide parts of the roots. Hence most of the examples given are from Trench C, which had plain glass, with squares engraved on it.

II. RESULTS.

(A) The Absorbing Root System.

It is convenient to discuss first the general life history of the absorbing root system of the apple, as seen through the glass windows of the observation trench. This will be followed by a more detailed, illustrated, description of the various phases of growth. Then the data on the seasonal cycles of root and shoot growth and their correlation with various seasonal factors will be shown by graphs and photographs, and finally certain quantitative data shown by the annual totals will be discussed.

(1) *Absorbing Root Life History.*

The young growing apple root, as seen in the observation trench, is white and succulent, with very short root hairs. At an age of usually between one and four weeks it begins to suberize. The root hairs shrivel up and the cortex turns brown. This portion of root is then presumably no longer absorbing. The cortex then shrivels and gradually disappears, leaving the central cylinder loose in the hole in the soil which the root has made. This central cylinder may develop secondary thickening and become a permanent part of the root system, bearing new roots as laterals, or it may rot away, as do many of the smaller roots. Thus the absorbing root life history is clearly seen. The root grows into a certain piece of soil, it absorbs water and other materials from it and then its absorbing organs die away. Its growing tip may meanwhile have passed on to other regions. Lateral roots may arise at a later date and new roots may come again through the same soil. Thus, the roots comb the soil through and through, wave after wave, each small area of soil alternately becoming relatively exhausted and then recuperating. This cycle of events is probably largely due to the action of hydrotropism and chemotropism.* When absorption has taken place for a week or so in one spot—particularly when the whole soil is becoming dry—a high moisture-tension area arises, through which, as other work has shown (Rogers (11), Veihmeyer (19)), moisture and dissolved salts will travel only very slowly. It is thus advantageous to the root to change the position of its absorbing area, and it grows on into fresh soil, allowing the old root hairs to die away.

A general idea of the appearance of the roots can be obtained from Fig. 3, Plate III, which shows part of an observation window against which the roots of Lane's Prince Albert on rootstock No. XVI were growing in June. The various phases of root growth can be seen; and a more detailed view is given in Figs. 4 to 17 described below.

* The term tropism is used here in the sense not merely of turning, but also growing towards or away from the stimulus, as described by Strasburger (1930).

(2) *The Growing Root.*

The growing root tips of the apple vary greatly in size, from minute barely distinguishable roots of a diameter of about 0·3 mm. to bold white roots of a diameter of 2·0 mm. or more. In Fig. 4, Plate IV, which is a photomicrograph of a growing rootlet of rootstock No. I, magnification 4·8, the root cap (A), the cell division and cell elongation region (B) and the root hair region (C) can be seen. The root cap is rather darker than the elongating portion. The wearing away and change of shape of the root cap as it is pushed through the soil can be observed in Fig. 5, Plate IV, which shows the same root two days later. The thick white vertical line to the right of the photograph is one of the lines engraved on the glass. It can be seen that this root has grown at the rate of 3 mm. per day. This is by no means unusual for the period of maximum root growth (usually July). Roots of stock No. XVI (very vigorous) have been observed growing at an average rate of 9·4 mm. per day for over a week. The mean extension rate of all the white roots in a trench in any one week varied from nil to about 25 mm. per root. The periods of maximum growth corresponded to the times when the soil was both warm and moist, as will be discussed later.

(3) *Suberization.*

After a period varying from about a week in hot dry weather to a month in cool moist weather, a marked change is seen in the root. The cells of the endodermis and primary cortex become suberized, the root hairs shrivel and the cortex turns brown and shrinks. The old cortex is then presumably merely acting as a protective sheath for the central cylinder, until a newly-developed cork-cambium has formed a corky rind which will protect the root and grow with it when secondary thickening sets in.

The suberization may spread as a wave down the root, or it may occur in patches along several inches of root simultaneously. This is shown in Fig. 6, Plate V, which shows the same root as in Fig. 5, Plate IV, but twenty-four days later. The cortex has become suberized and is shrivelling up. The root, originally about 1·69 mm. in diameter, has shrunk to 1·23 mm. diameter, and has become loose in the soil. The records show that the root cap had grown a further 60 mm. along the glass by August 10th, and then turned away. A soil insect (D) (*Collembolon* sp.) is seen on the shrivelling cortex, eating it. This feeding of insects has repeatedly been observed under the binocular microscope. A further stage is shown in Fig. 7, Plate V, taken seventy-eight days later, on October 31st. The cortex is now rotten and beginning to slough away. The central stele is just beginning to show (E). A further developed example of this phase is seen on the smaller root (F) which was formed in the first week

in April 1933, became suberized by April 27th, and by October 31st had its central stele well exposed. This was rather a smaller root than the other at the outset.

In Fig. 7, Plate V, it can be seen that a worm has made its way along the shrivelling root. This is typical of what frequently happens, and is quite easy to understand, for the passage made by the root offers a convenient path to the worm, quite apart from the decaying vegetable matter which it provides. This deep cultivation, afforded both by the growing and shrinking rootlets themselves and by the worms and other soil insects, must be of very great importance in the aeration and drainage of the soil. In the writer's excavation work, it has frequently been noted that roots were growing along a worm hole, and it was concluded that the root found the hole an easy passage and grew along it. While this probably often happens, the converse undoubtedly also takes place, i.e. the worm-burrow is made along a root hole. Fig. 3, Plate III, shows an example (W) of both happenings. A worm has made its burrow along the hole left by the shrinking of two roots that grew two years previously (laterals from these roots can be seen) and a new root, on reaching the worm hole, has turned down it. It was noted that sometimes the movement of the worms or other soil animals breaks the small rootlets, and then the portion of root below the break dies.

(4) *Lateral Roots.*

Small laterals may develop, both on unsuberized and on suberized roots. Fig. 8a, Plate VI, shows two roots, formed between July 11th and 16th, on July 18th, 1931, from both of which laterals have recently emerged or are just emerging. In Fig. 8b, Plate VI, nineteen days later, the laterals have grown out, and the beginning of suberization is seen. A further twenty-nine days later, Fig. 8c, Plate VI, the original roots are completely brown and a new root has pushed along the path left by one of the shrunken old roots.

Laterals and sub-laterals can be formed in quite a short time, as shown in Fig. 9, Plate VII. The largest root was formed on June 17th, 1931, and was brown on July 11th. Roots of the second order were visible on July 2nd, and of the third order on July 7th. The development of root hairs appears to be particularly intense on these small laterals.

Fig. 10, Plate VII, shows laterals growing in June 1932 from a suberized root formed in September 1931. Dying laterals (LL) of the previous year can also be seen indistinctly, and the central cylinders of other roots (K), exposed by the sloughing cortex.

Fig. 11, Plate VII, shows two laterals growing from a six-year-old root which has developed considerable secondary thickening. One further type of lateral is found in cases where an old lateral does not entirely shrivel up, but

continues to produce small sub-laterals year after year as shown in the diagram, Fig. 12, Plate VII.

Thus, laterals may develop both when the root is young and succulent, and when it has become suberized and after thickening has set in. The exact cause or stimulus which induces the formation of lateral roots at any particular place or time is not easy to determine. It was noted that when young roots were forced to change their direction, as, for instance by hard soil or by coming against the glass, laterals often developed at the point where the bend was made. (Compare Fig. 8, Plate VI.) It is possible that accumulation of certain substances at these points eventually causes laterals to develop.

The roots illustrated in Figs. 8 to 11 (Plates VI and VII) are all of rootstock No. I.

(5) *Classification of Roots.*

All the roots seen behind the windows are branches of the original adventitious roots of the vegetatively produced rootstock ; in this sense all are lateral roots. In view of the very obvious differences in size of new roots seen in the observation windows, however, the roots were grouped in two classes, termed mains and laterals. Mains were roots exceeding about 1 mm. in diameter, and laterals were smaller. In general it was found that the mains persisted, and the laterals did not, thus they probably correspond to the *Bereicherungswurzeln* (extension roots) and *Ernährungswurzeln* (feeding roots) respectively of von Alten (20). It was not possible to make a hard and fast division between mains and laterals however. Sometimes a small lateral would persist for years, and sometimes mains would die away. Sometimes a root would cease growing and become suberized to its tip and, later, recommence growth. Of course, the absorbing root system, which consists of all parts of the roots that are growing and bearing functioning root hairs, includes both mains and laterals.

(6) *The Root Hairs.*

The root hairs of the apple rootstocks used for these experiments are much shorter than in many plants. In the loam soil their length rarely exceeded 0·075 mm., and was more commonly 0·025 to 0·050 mm. (In sand, longer root hairs were observed.) One interesting feature frequently visible was what appeared to be a copious exudation from the older root hairs. Young root hairs (C) and older ones with globules of exudate upon them (C_1) can be seen in Fig. 13, Plate VIII, which shows a growing tip of a root of rootstock No. XVI (magnification about 12·6). The globules of exudate have coalesced into larger drops at C_1, and hide the root hairs themselves. The precise composition of this exudate has not yet been determined. It is composed partly of

water, for it turns anhydrous copper sulphate blue. It has been seen frozen on the root in the depth of winter. It has been seen at all seasons of the year, but is particularly copious when growth is at its height. It may help to dissolve soil solids, or it may possibly fulfil some other function. Further investigations on this matter will be undertaken shortly.

It is almost certain that this liquid is actually exuded, and not, for instance, merely condensed on the root hair, for in the early stages it can be seen in small droplets at the extreme ends of the root hairs. Such droplets can be seen in Fig. 14, Plate VIII, on the ends of the root hairs in the region marked C, where the root hairs appear to have small knobs on their extreme ends.

The young root hairs are of a translucent white appearance, but grow yellowish as they get older. It is very difficult to say exactly when they leave off absorbing, but for the purposes of this investigation it was taken that until they definitely shrivelled and turned brown they could absorb. Thus, in Fig. 8a, Plate VI, it would be reckoned that all of the root was in an absorbing condition, but in Fig. 8b most of it was not. Fig. 8b illustrates another interesting point. When suberization begins, the exudation from the old root hairs sometimes leaves on the root a covering of small waxy looking white scales, which may persist for some weeks. Some of these scales can be seen in Fig. 8b. The exact nature of this substance is also unknown, and it gradually disappears when the root rots away, as in Fig. 8c.

In Figs. 13 and 14, Plate VIII, the arrangement of cells and the differentiating vascular strands can be seen indistinctly. They can be more clearly distinguished in most of the larger young growing roots with the binocular microscope.

(7) *Secondary Thickening.*

The number of roots that developed rapid secondary thickening was relatively small. Such can be seen in Figs. 3 and 11, Plates III and VII. Some roots appeared able to function and produce laterals for months or even years without thickening appreciably. Further observations are being made on this point, by means of a microscope with a micrometer eyepiece, but this is not a very easy matter because as the root swells its centre is naturally forced to recede from the glass and it becomes more difficult to see the edges.

(8) *Death of Roots.*

As already stated, the majority of the lateral roots did not persist, the whole root usually rotted away gradually within a few months of suberization. A number of mains also disappeared in the same way. This is, perhaps, not surprising, for if all the rootlets persisted, the soil would gradually become full of them. The life history of the feeding roots appears closely comparable with

that of the leaves. Once their absorbing function is over, most of them cease growth and rot away. Those that remain to form the scaffolding of the new root system develop a secondary cortex, and sooner or later secondary thickening sets in.

(9) *Soil Fungi.*

Soil fungi were frequently visible through the windows. Much mycelium can be seen, for instance, in Fig. 13, Plate VIII. The relationship between various fungi and the roots is not yet very evident, however. On a few occasions fungi appeared to attack young growing roots, and became established on them, but this appeared to be exceptional. The wooden walls of the observation trenches themselves were severely attacked by dry rot, against which the ordinary lead paint used gave little protection. Bitumastic paint, which appears to be more durable under such severe conditions, will be used in future trenches.

(10) *Rootstock Differences.*

No very marked differences were seen between the growing roots of the various rootstocks. All had the general appearance shown in the photographs. The greatest amount of growth and hence the greatest length of white root was generally seen on the roots of No. XVI, but No. I and No. IX, at their peak periods, also produced quite large white roots. A pinkish coloration near the root tip was more frequently seen in the roots of No. I than in those of the other rootstocks. The root hairs of all the stocks looked similar, and the suberizing roots showed no large consistent differences. It was when the roots developed secondary thickening that some qualitative difference became apparent. Then the No. IX roots often showed a more yellowish colour than those of No. I or No. XVI. The relatively thick secondary cortex characteristic of No. IX does not, however, become apparent until the root is cut. The qualitative appearance of the roots, as seen through the windows, did not, therefore, supply any clue to their characteristic effects upon the branch system.

(B) Root Growth in Relation to Other Factors.

Weekly records of root growth were made from the time the trenches were installed onwards, as previously described. The amount of data thus accumulated was very considerable, but for the sake of brevity and in order to give the most comparable data, it is proposed to discuss the records obtained in the four years 1933 to 1936 inclusive, and to omit those made in 1931 and 1932, when the trenches were installed. Thus the risk of abnormal results due to damage done to the root system in installing the trench is lessened. It was observed that the effect of cutting a number of main roots, when the trench was installed, was to check the tree growth to some degree, but it caused a considerable stimulation

of new root growth from the cut ends. Thus, in the summer following the installation of the trenches, the glass windows showed a greater concentration of new white roots than was seen in subsequent years, and the average rate of growth per root was also somewhat greater in the first season. These effects were probably partly due to the breaking up and excellent aeration of the soil before repacking against the glass. By the end of the first season this abnormal stimulation had apparently disappeared.

The new root growth, total unsuberized root, and new shoot growth of Lane's Prince Albert apple on rootstocks Nos. I, IX and XVI, as recorded at weekly intervals throughout the year, together with the mean soil temperature, the mean soil moisture tension, and the weekly rainfall are shown in Fig. 15 for the years 1933 to 1936.* In these graphs, the scales for shoot growth, rainfall, soil temperature and soil moisture tension, are constant throughout the series, but those for root growth and unsuberized root, though identical for the three rootstocks within each year, have been changed from year to year, as indicated. This is because the root growth seen through the glass varied so much in different years. In 1933 and 1936 there was a medium amount of root growth, and the same scale was used for these two years. In 1935 there was a much increased amount of growth, particularly in the No. IX and No. XVI, which was probably mainly due to two causes. First, in the No. IX and No. XVI trenches, the soil, which was observed to be rather loose in 1934, was removed, air-dried and repacked behind the glass (which was moved two to three inches nearer the tree) in March 1935, during the period marked R on the graph (Fig. 15c). This accounts for the complete absence of visible roots in these two trenches in April 1935, followed by a very rapid increase in May. Secondly, in the middle of the blossoming period, at the point marked F, a disastrous frost destroyed the whole apple crop. The food materials which would normally have been used in producing a crop were therefore available for increased and longer sustained vegetative growth.

The records refer to the same trees throughout the period, with the exception of the No. IX in 1935. There were two trenches beside No. IX trees, D1 and D2. The records from them generally corresponded well, but the tree of D1, records from which are shown for 1933, 1934 and 1936, usually had rather more root than that of D2. In 1935, the D1 tree showed such a great stimulation of growth after the windows had been re-set, that the D2 tree records are shown, since it is considered that they give a fairer comparison. No. IX rootstock is apparently less suitable for the root observation method than No. I or No. XVI, for its roots did not grow very readily against the observation windows in most years.

* These four graphs are made from, and show the data given by, four tables each of 14 columns and 52 rows. The diagrams therefore present the data in a much more compact and more easily comparable form.

The figures for "inches of root" refer to total length visible against an area of glass of 720 square inches, recorded weekly. The No. I trench had a slightly larger window (840 square inches) in the position comparable to those of the No. IX and No. XVI trenches, and its figures have been adjusted to bring them to a comparable area. Thus, the figures for the three rootstocks are reasonably comparable, but it should be borne in mind that the No. I tree was checked more severely than the No. IX or the No. XVI, as more roots were cut when installing the trench, which had larger dimensions. This check is reflected in the reduced shoot growth of the No. I in 1933, 1934 and 1935, when it was actually less than that of the No. IX. The temperature and moisture tension records were taken in the trench beside the No. XVI. The 1936 moisture tension records are the only complete set. In previous years the instrument was only being developed, and various faults caused breakdowns; but the available records are included as they are of some interest. The relations between root growth, temperature and moisture will be discussed in a later section.

(11) *Root Growth, Shoot Growth and Season.*

From Fig. 15 it is seen that there was very little and sometimes no new root growth (thick line on graph) in the months November to February in the years 1933 to 1936. Some root remained unsuberized throughout the winter in some years, particularly 1932-33 and 1935-36, but it is clear that while there was usually some root activity during the winter, it was relatively small. The beginning of a definite increase in growth was usually seen in March and April, and root growth increased rapidly in May and June to reach a peak in June or July. This was usually followed by a smaller peak a month or so later, and then growth slowed down. A slight increase in growth usually followed the autumn rains, and in some cases this was quite considerable. It is clear that the period of greatest root growth was usually early summer.

In 1935 vigorous root growth continued till the end of September, and growth did not cease throughout the winter. This was probably mainly due to the absence of a crop of fruit, as already mentioned (the three seventeen-year-old trees bore fifteen apples between them), but was doubtless also assisted by the early autumn rains.

Shoot growth, i.e. new leader growth, began in May each year. It usually reached a peak in June and slowed down rapidly, to end in August. The first spur leaves appeared just before the blossoms opened. In 1935 shoot growth continued about a month longer than in the other years, but leaf fall occurred at about the same time as in 1934.

Thus, active root growth began a month or two before shoot growth and continued after shoot growth had ceased.

(12) *Rootstock Effect.*

The most obvious difference between the different rootstocks was in amount of root growth, which followed out the already well-known vigour characteristics of the stocks. The dwarfing No. IX generally showed least root growth, and the very vigorous No. XVI, most root growth. In 1935 there was a little more root growth against the No. IX than against the No. I windows, doubtless due to the re-installation of the former, as already mentioned. The records therefore follow the lines that would be expected from previous work, which has shown that the root : shoot ratio, under given conditions, is nearly constant, irrespective of the size of tree (Rogers and Vyvyan (15)).

A less obvious, but very interesting, difference was in period of root growth. In general it will be seen that the most vigorous stock, No. XVI, had reached its first peak of growth some time before the least vigorous, No. IX ; and the No. I, though nearer to the No. IX than to the No. XVI, was generally intermediate. Thus, in 1934 and 1936, the No. XVI rose to its highest peak of growth and of unsuberized root more than a month before the No. IX. In 1935, when the windows were re-installed, the difference was less, viz. only a week, but in 1933 it was barely visible.

The period of cessation of root growth was generally about the same in the different stocks, though No. I appeared to have a tendency to slow down rather more gradually than the others. If further research shows that the more vigorous rootstocks always tend to reach their maximum root growth before the less vigorous ones, new light will be thrown on rootstock effect. A stock that has its absorbing root system well developed and well distributed by the time the more stringent conditions of midsummer arrive is obviously in a better position to maintain a large and vigorous branch system than is one which starts later. Whether this factor is a primary cause, or merely an effect, of rootstock influence it is very difficult to say. The records of growth against the other windows in the root observation trenches (made at monthly intervals), support the above data strongly, and some further support is given by unpublished records obtained in a preliminary trial with stocks No. I and No. II in root observation boxes ; but the matter clearly needs further investigation.

In period of shoot growth there was no appreciable difference between these mature trees on different stocks.

(13) *Root Growth and Soil Temperature.*

Perhaps the most striking correlation shown in Fig. 15 is between soil temperature and new root growth. First it is seen that active root growth usually begins as the mean soil temperature reaches about 45° F. This agrees with the findings of Nightingale (9) with apple and peach trees in sand cultures. After root growth begins, it increases or decreases almost week by week with

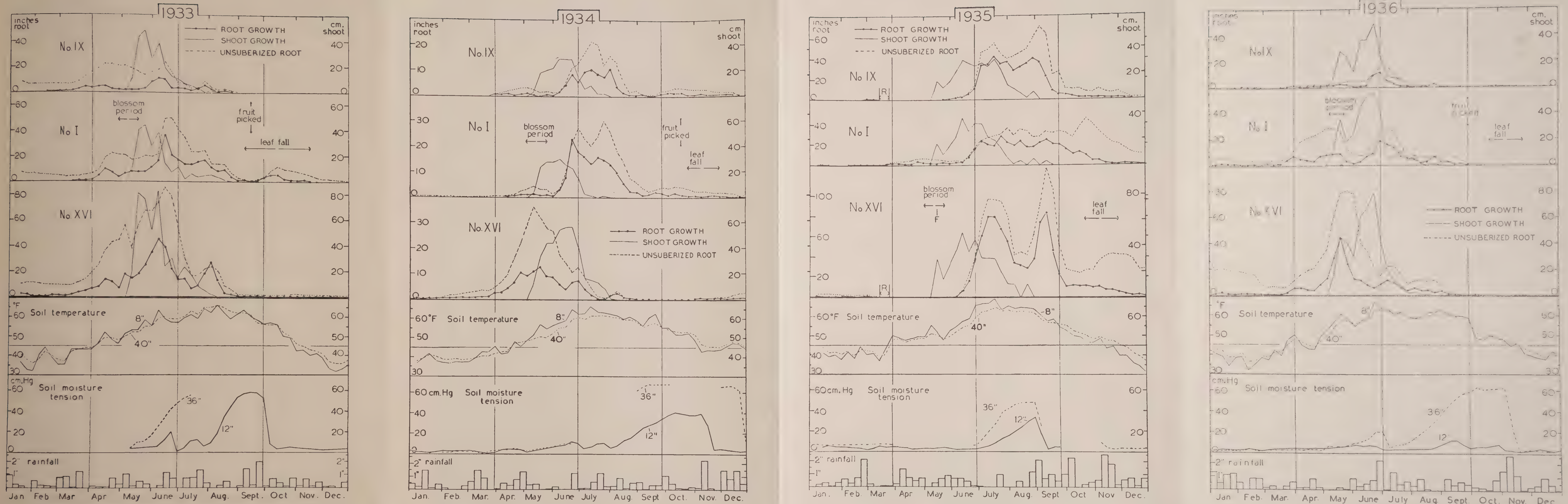


FIG. 15.—Relationship between soil factors and root and shoot growth.

(a) 1933.

(b) 1934.

(c) 1935 (re "R" and "F" see text).

(d) 1936.

increase or decrease of soil temperature. The deeper layers of soil vary more gradually in temperature than the top layers, and since the temperature (and also moisture) figures are the weekly mean of daily readings the response to their changes may be seen either in the same week or in the following one, according to whether the main changes occurred at the beginning or the end of the week. But, at any rate in the early months of the year when water is plentiful, the correlation between soil temperature and root growth can be followed out in all the graphs. It should be noted that in the early part of the year root growth responds to temperature changes before there are any leaves on the tree, hence it is likely that the temperature effect is a direct one, and not merely indirect through increased stimulation of leaf activity by sunlight and warmth. The response to rise and fall of temperature is greater and more rapid in the more vigorous rootstocks, as already noted.

As the summer proceeds, a new factor becomes apparent. The graphs show a very marked decline of new root growth, although the soil is relatively warm, often above 60° F. at 40 in. There is some evidence in the soil moisture tension records to suggest that this decline may be due, at least in some cases, to drying of the soil. Before this is discussed in detail, a review of the moisture conditions is required.

(14) *Soil Moisture Records.*

These records are less simple to interpret than those of temperature, but are certainly of great importance. Rainfall was recorded on an open meteorological plot, some 500 yards away from the trenches. The total figures are reasonably applicable to the root trenches, but the exact distribution over the soil, during the months when the trees were in leaf, was certainly far from uniform. The moisture meter pots were placed at the east side of the observation windows, some 36 in. from the trunk of the No. XVI tree, and their readings obviously apply directly to this part of this tree only. Soil moisture conditions vary greatly from place to place in the soil, as other work has shown (Conrad and Veihmeyer (4)), depending largely on root concentration and exposure to rain. There is some evidence that the root concentration near the moisture meters was less than in other parts, so that the moisture tension registered was probably rather less than that existing in some other parts of the soil. Nevertheless, in the absence of fuller data, the present limited records are of interest.

The soil moisture meter, though originally devised and developed specially for this investigation, has already proved of much wider interest. Here it is sufficient to recall that the meter registers the soil moisture tension, which may be regarded as the force with which the soil retains its moisture. This is measured by means of a water-filled porous pot, buried in the soil at the required depth, and connected to a mercury manometer or vacuum gauge, which is thus

linked to the water films round the soil particles. The special devices needed to avoid errors through freezing and infiltration of air have been described elsewhere (Rogers (11)). The soil moisture tension is 0 at saturation and usually 4 to 7 cm. Hg at "field capacity"; it rises as the soil dries, and falls as the soil becomes wetter. At about 60 cm. Hg, the limit of the meter's range is reached, and at this point on the scale the actual moisture tension may be 60 or more.

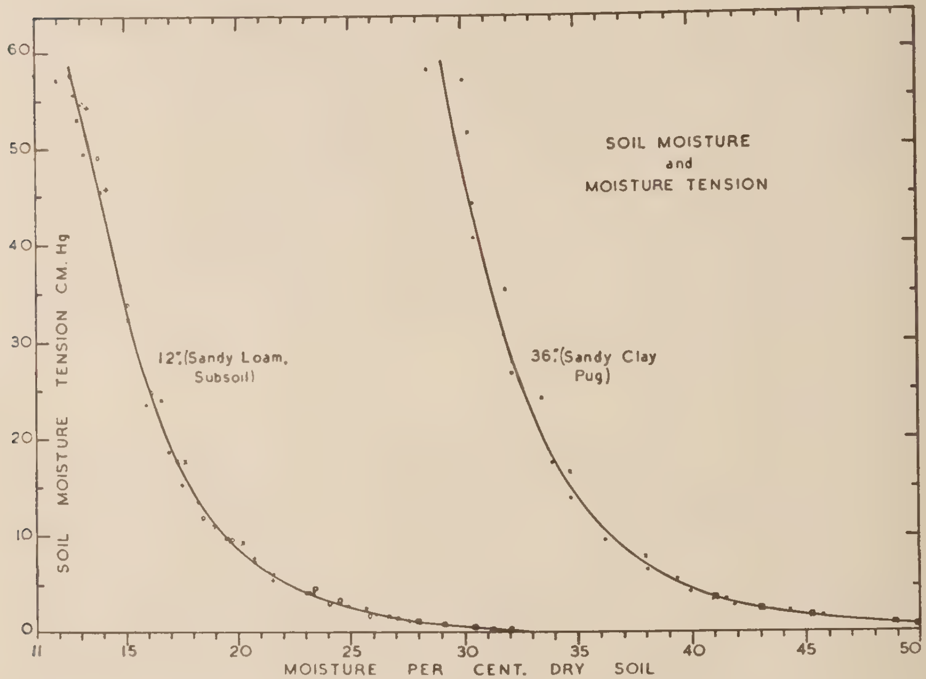


FIG. 16.

Calibration curve for moisture tension meters in sandy loam sub-soil and sandy clay "B" horizon. Each set of symbols gives results of a separate test.

A calibration curve (made on samples in the laboratory) showing the relation between soil moisture tension and actual moisture content of this soil, at 12 in. and 36 in., is shown in Fig. 16. It can be seen at once that a given tension is exerted by a fine-grained soil at a much higher moisture content than exists in a coarse-grained soil showing the same tension. It will be appreciated therefore that the soil moisture tension is a more useful figure than the moisture percentage, as it eliminates the complications introduced by different soil textures at different depths and gives a value which is probably reasonably comparable over a fair range of textures.

The closest correlation between rainfall and soil moisture tension is shown by the daily readings given in other papers, but, for simplicity, weekly means are given in this paper, since they show the broad tendencies more clearly.

The moisture tension records in Fig. 15, incomplete though they are, show that in the winter the whole soil block becomes filled to the field capacity. The soil in this orchard at East Malling, however, approaches saturation only for a few hours after very heavy rain, on account of the free-draining Ragstone rock below. At depths of 12 in. and more there is practically no appreciable drying out until the trees are in full leaf in May. From then onwards, in spite of a relatively well-distributed and copious summer rainfall, the deeper layers of soil beside this mature tree whose roots fill the whole soil block (Rogers and Vyvyan (15)), dry out steadily, and at 36 in. the soil usually remains relatively dry until the leaves fall and the autumn and winter rains set in. The summer rains may be sufficient to remoisten the soil to a depth of 12 in. from time to time, as in 1933 and 1934, or they may even entirely prevent much drying out at 12 in., as in 1936 ; but these rains are normally insufficient to penetrate to 36 in. This emphasizes the point that water applied to the surface of the soil does not become distributed evenly through the whole soil block, but wets a limited depth to the field capacity, further spread being almost negligible, as shown by Veihmeyer (19). The idea that it is the deep roots that maintain the tree in drought periods is seen to require some qualification, therefore. In a young tree, whose roots are near their point of origin on the rootstock (and therefore relatively shallow), it is clear that this area will become dried first ; and the roots, unless prevented by other factors, will grow towards moister areas, both horizontally and downwards. The roots may soon meet laterally, leaving only the deep layers unoccupied, and then it would be true to say that the deeper layers of soil provided the tree's main water supply in a drought period. After a few years, however, the whole soil block becomes permeated with roots, as in the orchard under review, and then, as the records show, the deeper layers actually reach dry conditions before the shallower layers, because the latter are more quickly replenished by rain. Of course, even in this case, the deep roots certainly contribute to the tree's drought resistance, because the water drawn from the lower layers in the early part of the year helps to conserve the supply in the shallower layers. But when rainless periods occur in late summer, the moisture records show that the deep roots are then actually under drier conditions than the shallower roots.

(15) *Soil Moisture and Root Growth.*

In 1933 (Fig. 15a), it is seen that the falling off of root growth of all three trees in June, with the soil temperature between 55° and 60°, coincides with the sharp rise of soil moisture tension at 36 in. and 12 in. Rain later remoistened

the soil to 12 in., and an increase of root growth is seen in the following weeks, while further drying at 12 in. in mid-August (the 36 in. layer remaining dry, as subsequent work confirmed) is reflected in a rapid fall of root growth, although the soil remained at a temperature of nearly 60° F. Re-wetting at 12 in. in early October was followed by a new burst of root growth in the No. I tree, but only slight growth occurred in the No. XVI.

The precise period in 1934 when drying at 36 in. became severe was unfortunately not recorded by the meters, owing to a breakdown, but by July 19th it was noted that the soil behind the glass looked very dry, and this was confirmed on August 9th. In this period the No. XVI root growth fell off to zero, and that of the No. I and No. IX also fell off. By August 16th the soil behind the glass was cracking. Some meter readings in September showed a tension of over 60 cm. Hg at 36 in., and a rapidly rising tension at 12 in. also. The remoistening of the soil in November and December was probably too late to permit active root growth, although the soil temperature was about 45° F. The fall in growth rate of the No. XVI tree in early June is anomalous and does not fit either the rising temperature or the relatively good moisture conditions indicated.

In July 1935 a rapid decrease of root growth occurred in the No. XVI tree, accompanying an increase of soil moisture tension from about 20 to 40 cm. Hg at 36 in., with a smaller rise at 12 in. Heavy rains at the end of August and the beginning of September remoistened the soil to 36 in., and at once a rapid increase of root growth is seen in the No. XVI tree, although the temperature was falling. This growth rate soon fell off again, in agreement with the falling temperature. Unfortunately the moisture tension records are again incomplete, but it is unlikely that the soil dried much after September, as the rainfall was so heavy. The No. I and No. IX root growth records in 1935 do not show much agreement with the moisture records (obtained in the No. XVI tree trench) and it is possible that these smaller trees suffered no water shortage in that year.

The year 1936 had a remarkably wet summer, and there was practically no drying out in this cultivated orchard at a depth of 12 in. A rise of tension to 20 cm. Hg at 36 in. in June was reversed by heavy rains, but the soil dried out to 60 cm. Hg at 36 in. by September. In this year also it appears that moisture was ample during the growing period, and temperature was the main controlling factor. Thus it appears that, even under English conditions, lack of soil moisture may be a limiting factor to root growth in some years. The exact point at which a check in growth begins is not easy to determine from the present studies, but it seems clear that a moisture tension of 40 cm. Hg, and in some cases even less, is sufficient to exert an appreciable retarding effect. In a previous study with sandy soil (Rogers (10)), marked retardation of root

growth was noted at a moisture tension below 30 cm. Hg. In any case it is clear that retardation of root growth occurs long before the wilting point is reached. No wilting was observed on these trees, or on weeds below them. This suggests that the theory of Veihmeyer (19), now widely repeated in many works on irrigation, that water is equally available to the plant throughout the range between field capacity and the wilting point, may require some modification.

(16) *Other Factors.*

While soil temperature and moisture appear to be very significant factors in root growth, it is unlikely that they are the only important ones. Accumulation of CO_2 in the soil, as suggested by Cannon and Free (3), and also depletion of inorganic nutrient materials, may also be powerful factors. Variations in the elaborated food supply from the leaves, and especially its reduction in amount as the days get shorter and during defoliation, must also have a large influence. The latter point was clearly shown by Heinecke (7). Any or all of these causes may have contributed to the sudden fall in new root growth seen in the graphs towards the end of each season. All these factors clearly need further investigation.

(17) *Shoot Growth and Temperature.*

It is readily seen in Fig.15 that the variations in shoot growth rate (thin solid line), in the first part of each growing season, correspond with variations in the soil temperature at 8 in. Doubtless both are mainly dependent upon radiation, itself mainly due to sunshine. While shoots would become warmer than the soil at 8 in. by day, they would get colder at night. Thus the soil temperature at 8 in. appears to give a convenient rough indication of the general speeding up and slowing down of growth processes, due to radiation. As the season proceeds, shoot growth falls off rapidly in spite of the increased temperature. The shoot growth period was about a month longer than usual in 1935, when there was no fruit, which suggests that the swelling of the crop may absorb much of the energy of the tree. Indeed it is well known that cropping and growth are, to a certain extent, antagonistic. The final ripening of the wood and dormancy are probably due to the combined action of several factors.

(18) *Unsuberized Root.*

The thin broken line in Fig. 15 shows the total length of unsuberized (i.e. white) root seen through the windows each week. In general, this follows the rise and fall of new growth, sometimes with a lag (especially in falling) of about a week. Taking the unsuberized root length in conjunction with the new root length, the rate of suberization can be deduced. Where the mean length of unsuberized root during any long period is equal to the length of new root,

the average time of root suberization is equal to the observation intervals (in this case one week). When the length of unsuberized root exceeds that of new root, the mean suberization time is more than a week, and so on. Similarly, when the lines of unsuberized and new root diverge, total growth is faster than total suberization ; and when the lines converge, suberization is faster than growth.

In the winter and early spring, suberization is very slow, so that a root that grows in the early months of the year remains unsuberized for several weeks, often over a month. As growth quickens, suberization also becomes more rapid, reaching an average of one to two weeks in the summer, and finally slowing down again in the autumn. In general, it is seen that rate of suberization corresponds closely with temperature. High temperature, and, especially, rapidly rising temperature, appears to cause a quickening of suberization.

The effect of dry conditions is not very easy to separate from the effect of warm conditions, in this case, as both sets of conditions usually occur together. However, there are indications that drought adds to the speed of suberization. This might, indeed, be expected, since absorption becomes increasingly difficult as the soil becomes drier.

Here a paradox is seen. In several cases the amount of unsuberized root seen through the windows fell to nothing in periods when the tree was still undoubtedly actively transpiring, and the soil, as shown by the meters, was still drying. This is probably a reminder that the visible roots are only a relatively small sample of the vast absorbing root area of the tree, and that roots away from the glass and perhaps especially at different distances from the trunk, may be behaving differently from the samples under observation. This would apply with particular force to young trees which can constantly extend their root systems into previously untapped soil. In older orchards, where every cubic foot of soil has already been combed through and through by roots, the variation would probably be less. Direct weighing of fibrous root of excavated trees by Rogers and Vyvyan (15) has shown that, in uniform soils, in mature orchards fine fibrous root concentration is relatively uniform.

Possible explanations of the complete lack of unsuberized root observed at certain times may therefore include the following : (i) that the roots are then growing in other soil areas, (ii) that the rise and fall of growth and suberization at the windows are somewhat exaggerated by the fact that temperature variations at the observation windows are rather greater than in the main soil block, (iii) that the longer exposure of the windows to light, needed for recording observations on the large numbers of roots that grow in early summer, causes these roots to suberize more quickly than those in the main soil block. Exposure to light tests supported this idea. A further suggestion, that roots can still absorb appreciably when suberized, appears very unlikely. The work

of Scott and Priestley (16) shows that absorption is confined to "the area lying between the apical meristem and the regions with completely suberized membranes".

Whatever the cause, it probably reflects the imperfection of experimentation; but the trouble is fortunately apparent only in a small proportion of the observations.

(19) *Relation Between Number and Length of Roots.*

The upper part of Fig. 17 shows the fairly close relationship existing between number and length of root growths recorded each week for No. XVI in 1936. Graphs could have been made for all the trenches each year to show the same point. There is, however, a certain amount of variation in rate of growth per root from week to week. The rate usually increases with rising temperature under moist conditions, hence the main peaks of growth are due to an increase both in number of roots and in average length. Sometimes the average length increases when the number is falling, however, and here other factors appear to be involved. It is seen, therefore, that the number of roots alone, a record of which can be made much more quickly than that of root lengths, could be used for many comparisons, but the number does not give such full information as the length, and records of both are desirable for complete information.

(20) *Root Growth at Different Depths.*

The second part of Fig. 17 shows the number of growing roots seen through the upper and lower observation windows of the No. XVI trench in 1936. Taking these curves in conjunction with those for soil temperature and moisture shown below in the same figure, it can be seen that there is quite a marked local response to different soil conditions, as well as the general response discussed previously. Thus, from January to March the lower layers were warmest, and root growth (such as it was) was mainly in them. As the top soil warmed up in April and May, root growth became greatest in these layers. Then, as the lower layers became drier at the end of June, growth decreased, although the temperature was high, to increase again after remoistening in July. The graph shows remarkably good correlation throughout for such a relatively small sample. Similar local correlation was seen in other years for this tree.

The local response was less obvious with the No. IX and No. I trees, but as the only detailed temperature and moisture records were those on the No. XVI tree there is no very accurate comparison. There is little room for doubt, however, that individual roots do respond locally to the precise soil conditions surrounding them, though their reaction must obviously also depend on what is happening to the tree as a whole.

(21) *Quantitative Data.*

(a) *New root growth.* Table III summarizes the annual totals of number and length of roots, as recorded weekly at the observation windows, and also shows the distribution in the upper and lower layers of soil. The number is given as "new root extensions" rather than as "growing roots", since the increase of a root that made new growth each week in, say, four weeks, would be recorded as four extensions. The figures for window C1 have been adjusted to an area comparable with that of the other trenches, as before.

The contrast between the stocks in both number and length of roots, the more vigorous stocks having the most root, is at once apparent, but it is seen that the mean length of growth per root is not very dissimilar. It is evidently through making more numerous, rather than by longer, root extensions that the vigorous stocks develop a greater absorbing area.

The variation in amount of growth from year to year and the much greater root length in 1935, when frost destroyed the fruit crop, can clearly be seen, and in this year there is not only an increase in number but also in mean length of root in all cases. It should be recalled that the No. XVI and No. IX windows were re-set that year, but the No. I window was not ; and examination of the figures suggests that, as the increase of growth was greater in the No. XVI and No. IX than in the No. I, it was partly, but certainly not entirely, due to this re-setting.

The total number of individual root records dealt with in this summary is over 9,000. For each of these roots the position, time and amount of new growth and unsuberized length were recorded. An almost equal number of records was obtained from the other observation windows in the trenches, but the results are not presented in detail, since they confirm those given here.

(b) *Unsuberized root.* The amount of unsuberized root is generally rather more than twice that of the new growth. Since the unsuberized root is made up from the past and current new growth, the ratio of unsuberized root to new growth, over a long period, gives a rough measure of the mean rate of suberization, in units of the observation interval, which was one week. The figures vary somewhat from year to year, but for the totals over four years the ratios work out as follows: No. XVI, 2·32 (weeks) ; No. I, 2·19 ; No. IX, 2·13. It is thus seen that the mean rate of suberization is similar, but over the whole period the very vigorous No. XVI shows a tendency to suberize slightly more slowly than the others. Experiments on the effect of light showed that prolonged exposure to light hastens suberization, hence all these figures may be a little low. Since many roots grew and became suberized in complete darkness within four weeks in the windows in which records were made monthly, however, it is likely that the values are not greatly reduced. The figures given in Table III are

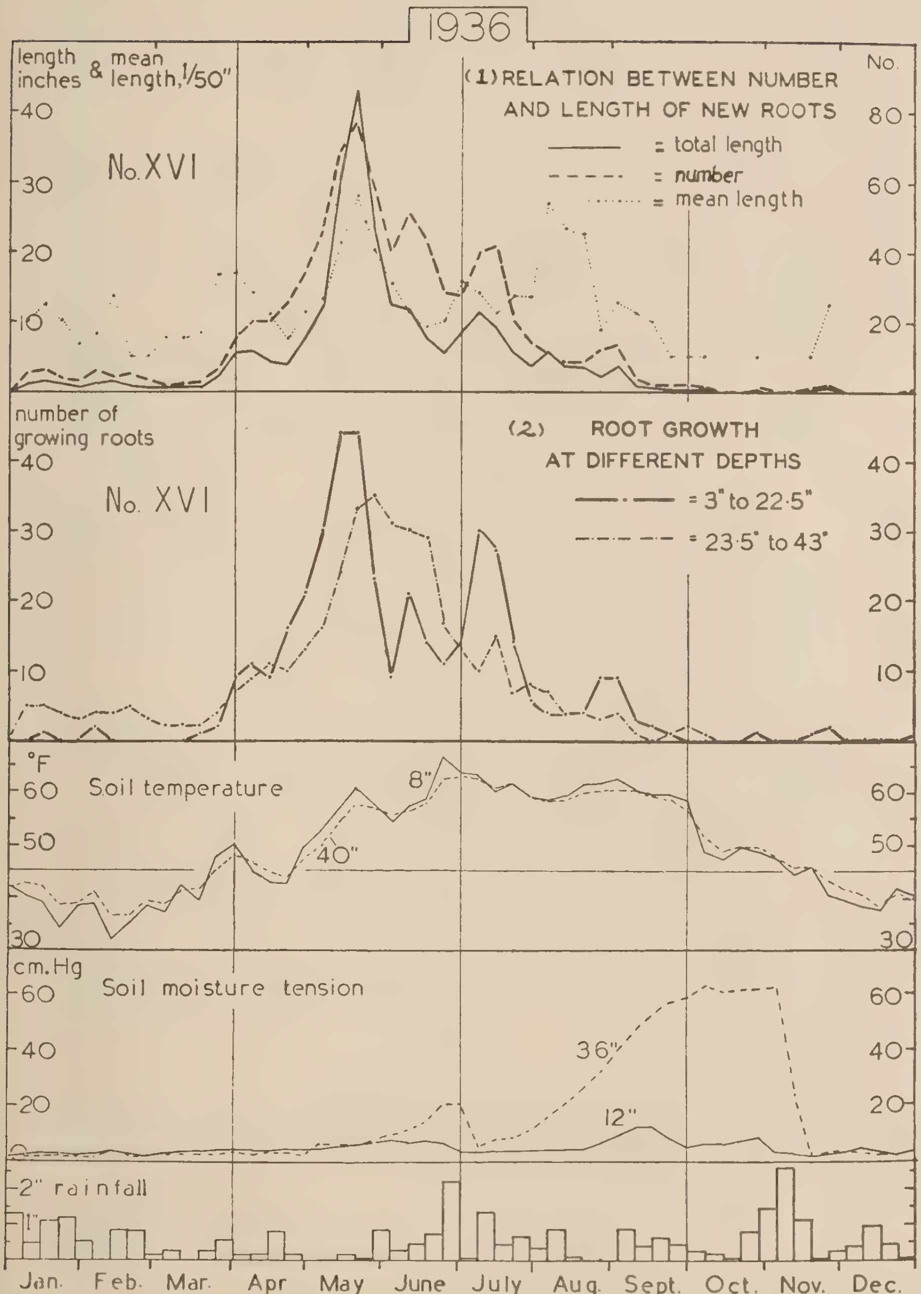


FIG. 17.

(1) Correlation between number and length of roots.
(2) Root growth at different depths.

TABLE III.

Amount and Position of Root Growth and Absorbing Root.

			Total amount of Root.					Growth at Upper Windows only.				
			New Root Extensions.			Unsuberized Root.		New Root Extensions.			Unsuberized Root.	
Stock.	Trench No.	Year.	Number.	Length inches.	Mean length per root (weekly growth).	Total length "week inches."	Ratio unsuberized root / new root.	Percentage of total number.	Percentage of total length.	Mean length per root.	Percentage of total length.	Ratio unsuberized root. / new root.
XVI	D3	1933	1288	382·0	·297	1005·6	2·63	60·0	67·3	·333	58·8	2·30
	,,	1934	534	113·7	·213	310·0	2·73	64·2	63·5	·210	43·1	2·44
	,,	1935	1885	856·3	·454	1529·4	1·79	58·9	59·8	·461	45·5	1·63
	,,	1936	788	242·7	·308	852·9	3·52	50·8	41·6	·253	34·8	2·94
	Mean		1123·7	398·7	·318	924·5	2·67	58·5	58·0	·314	45·5	2·33
I.	C1	1933	825	273·4	·331	617·0	2·26	71·1	64·4	·300	66·8	2·34
	,,	1934	531	161·0	·303	290·0	1·80	69·0	60·2	·265	60·5	1·81
	,,	1935	1140	391·5	·343	822·0	2·10	73·4	58·9	·276	58·2	2·07
	,,	1936	726	170·1	·234	453·8	2·67	72·6	59·7	·193	63·8	2·85
	Mean		805·5	249·0	·303	545·7	2·21	71·5	60·8	·258	62·3	2·27
IX.	D1	1933	280	82·4	·294	341·7	4·14	85·7	85·1	·292	79·8	3·89
	,,	1934	266	87·2	·328	194·6	2·23	87·2	85·3	·320	84·3	2·21
	D2	1935	877	430·0	·490	739·3	1·72	62·3	56·3	·446	56·0	1·71
	D1	1936	222	47·2	·212	101·6	2·15	87·3	79·9	·194	73·7	1·99
	Mean		411·2	161·7	·331	344·3	2·56	80·6	76·6	·313	73·4	2·45
	Total		9362	3237·5	—	7257·9	—	—	—	—	—	—
	Mean		763·5	269·8	·317	604·8	2·48	70·2	65·2	·295	60·4	2·35

the arithmetical means of the yearly ratios, and, while giving slightly different values, show the same point. The reason for the exceptionally high value for D1 in 1933, which raises the average so much, is not known.

(c) *Position of root growth.* The figures for percentage of root growth in the upper windows show that, while the proportion varied from time to time, on the average there were over twice as many roots in the top windows (3 in. to 22½ in.) as in the bottom ones (23½ in. to 43 in.). Much the highest percentage in the top windows is found in the No. IX in 1933, 1934 and 1936. Too much emphasis should not be placed on this, since the number of roots involved is relatively small, and they grew mostly from one main root. In the other No. IX trench the percentage in the top windows was much less, being only 18 and 17 in 1933 and 1934 respectively ; but here again numbers were very small. Excavation studies on No. IX trees adjacent to these (Rogers and Vyvyan (15)) showed that about 60% of the roots below 1 mm. diameter (classed as fibre) were more than 19 in. below the soil surface, hence it is probable that if a better sample of the growing roots could have been seen, a more even distribution would have been recorded. The percentage of new root of the No. XVI in the top windows is less than that of the other stocks (hence the percentage in the bottom windows is greater), showing that the general root distribution of No. XVI is rather deeper. This agrees with the excavation work already quoted. In No. I the percentage of total length in the top windows is much less than the percentage of total number, showing that the mean root length is less in the top windows than in the lower ones. This can also be seen by comparing the mean length per root in the upper windows with the mean length in both windows. In the No. XVI there is no consistent difference in root length in the two layers.

The percentage of unsuberized root in the upper windows is similar to the percentage of new growth, except for No. XVI, where it is appreciably less. This suggests that suberization in the upper layers may be rather faster than in the lower ones in this case. This is also evident in the " mean suberizing rate " in the upper layers shown by the unsuberized-root : new-root ratio, compared with that in both layers.

A good idea of the actual root distribution against the glass and the relative concentration of roots of the different stocks is given in Fig. 18, which shows the total root growth on comparable pairs of upper and lower windows in 1935. It is seen that although many growing roots were present at the very bottom of the windows, more than 40 in. deep, the greatest root concentration is between 5 in. and 20 in. deep, as the preceding figures have shown.

(d) *Mains and laterals.* Table IV shows the amount and distribution of main and lateral roots. The percentage of roots recorded as laterals varied

greatly from year to year, showing how difficult it is to fix a rigid standard for this record. In 1933 and 1934, it was 32% to 56% of the total; in 1935 and 1936, it was 46% to 88% (the latter in the No. IX). The mean percentage for the four years worked out at 43 for the No. XVI, 49 for the No. I and 61 for the No. IX. There was, as might be expected, a higher percentage of laterals in

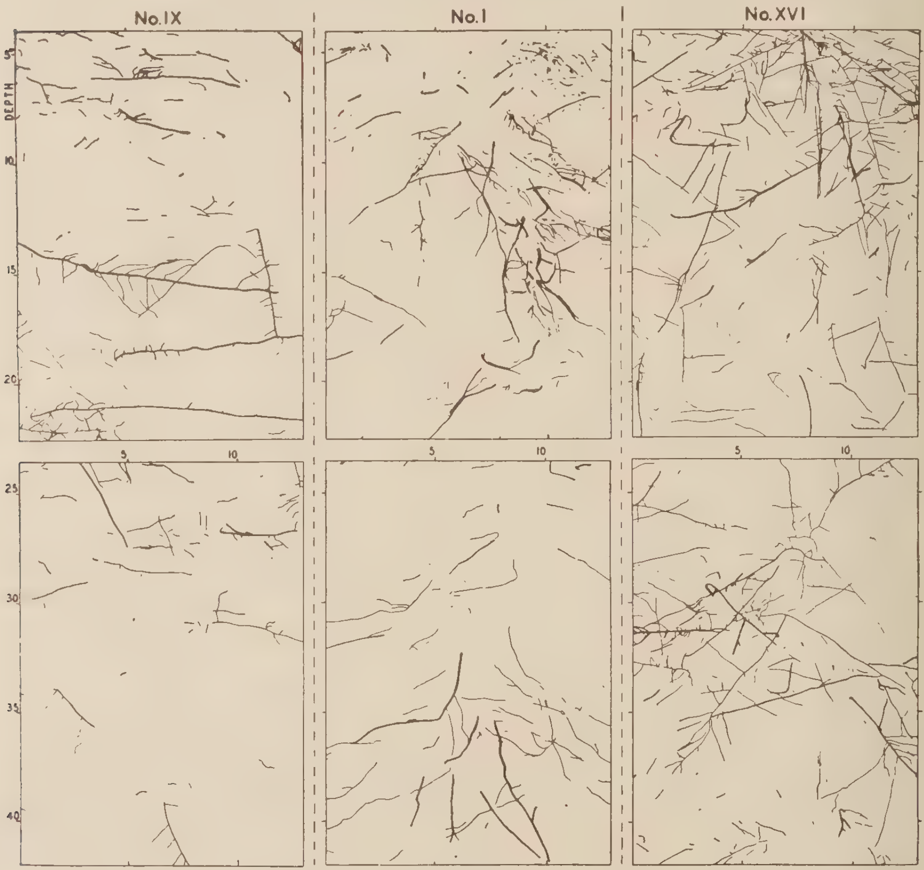


FIG. 18.
Root growth of M.IX, M.I and M.XVI on observation windows during the year 1935.

the upper windows, the mean being 75·5 of the total laterals. The mean length per lateral root did not vary greatly from stock to stock, and over all stocks and years worked out at 0·184 in. in the top windows and 0·228 in. in the bottom ones. For main roots the mean length was 0·433 in. in the top windows and 0·513 in. in the bottom ones, again showing the tendency to increased growth in length per root in the deeper layers.

Table IV.

Amount and Distribution of Main and Lateral Roots (lengths in 1/10 in.).

Stock	Trench	Year	Lateral Roots. As percentage of total number. Upper Windows	Lower Windows	Both Windows	Lateral Roots. Mean length. Upper Windows	Lower Windows	Both Windows	Lateral Roots. Total length. New.	Unsuberized.	Main Roots. As percentage of total number. Upper Windows	Lower Windows	Both Windows	Main Roots. Mean length. Upper Windows	Lower Windows	Both Windows	Main Roots. Total length. New	Unsuberized.
XVI	D3	1933	19·9	12·7	32·6	1·82	1·57	1·72	723	981	40·1	27·3	67·4	4·08	2·82	3·57	3097	9075
	,,	1934	23·8	8·1	31·9	1·35	1·26	1·33	226	327	40·4	27·7	68·1	2·55	2·44	2·50	911	2773
	,,	1935	31·7	20·4	52·1	2·66	2·78	2·70	2657	3686	27·2	20·7	47·9	6·89	6·09	6·55	5906	11608
	,,	1936	33·8	18·2	52·0	1·66	2·34	1·93	845	1555	17·0	27·4	44·4	4·24	4·69	4·52	1582	6974
Mean			27·3	15·7	43·0	1·87	1·99	1·92	1113	1637	31·2	25·8	57·0	4·44	4·01	4·28	2874	7608
Ratio Unsuberized : new									1·47								2·05	
I	C1	1933	24·1	9·8	33·9	1·67	2·23	1·83	597	861	47·0	19·1	66·1	3·68	5·03	4·07	2591	6339
	,,	1934	37·8	12·0	49·8	1·31	1·76	1·42	438	527	31·2	19·1	50·3	4·26	5·22	4·63	1439	2956
	,,	1935	38·3	8·3	46·6	1·90	3·90	2·26	1398	1800	35·0	18·4	53·4	3·70	5·93	4·46	3169	7786
	,,	1936	50·0	16·3	66·3	1·53	2·19	1·70	952	1784	22·6	11·1	33·7	2·80	5·26	3·61	1032	3509
Mean			37·5	11·6	49·1	1·60	2·52	1·80	846	1243	33·9	16·9	50·8	3·61	5·36	4·14	2058	5148
Ratio Unsuberized : new									1·47								2·50	
IX	D1	1933	25·7	5·0	30·7	1·33	1·35	1·33	115	202	60·0	9·3	69·3	3·61	3·96	3·65	709	3215
	,,	1934	49·6	6·4	56·0	2·04	1·64	1·99	297	485	37·6	6·4	44·0	4·74	5·94	4·91	575	1461
	D2	1935	45·2	25·9	71·1	2·95	3·75	3·24	2026	2690	17·1	11·6	28·7	8·35	10·01	9·02	2274	4703
	D1	1936	81·0	6·8	87·8	1·86	2·66	1·92	374	710	6·3	5·9	12·2	3·07	4·23	3·63	98	306
Mean			50·4	11·0	61·0	2·04	2·35	2·12	703	1022	30·2	8·3	38·5	4·94	6·03	5·30	914	2421
Ratio Unsuberized : new									1·45								2·64	
Total									10648	15608							23383	60705
Mean			38·4	12·8	51·2	1·84	2·28	1·95	—	—	31·8	17·0	45·8	4·33	5·13	4·59	—	—
Ratio Unsuberized : new									1·47								2·60	

Calculating the ratio of unsuberized root to new root for mains and laterals separately shows that it is much less for laterals than for mains. For laterals the mean for four years is similar for all stocks, being from 1·45 to 1·47. For mains it varies from 2·50 for No. I to 2·65 for No. XVI, the mean for all three stocks being 2·60. Thus it is seen that laterals have a much shorter absorbing life than mains. The full annual data for all four trenches are given in tabular form in the thesis of which this paper forms part, available at London University.

III. DISCUSSION AND CONCLUSIONS.

This work has shown that it is possible to observe growing apple roots in the field over a period of several years by the observation trench method described. The conditions, though to some extent artificial, are nearer to natural than might at first be thought.

It is clearly shown that individual absorbing roots are relatively short-lived. The absorbing root system is therefore constantly changing and constantly being replaced. In fact, the roots constantly comb the soil through and through. This fits in with the observations of Veihmeyer (19) and Rogers (11) that moisture (and presumably dissolved substances) move very slowly through the soil, except when it is near saturation point. Therefore the root cannot extract a rapid supply of water from distant parts of the soil merely by exerting a high suction, but must grow towards the moister areas. Hydrotropism and chemotropism are thus probably among the main root extension stimuli. This again agrees with the observations of Rogers and Vyvyan (15), Aaltonen (1) and Haasis (6), that root systems are relatively more spreading on sandy, i.e. poor and dry, soils than on others.

The shrinkage, death and sloughing off of the root cortex observed and illustrated, and the complete death and rotting away of small roots, is obviously a most important factor in the aeration and drainage of the soil. Here an interesting connection between root growth and insect and other soil organisms which feed on the rotting roots is demonstrated. Larger insects and other animals such as earthworms also enlarge the passages made by the decaying roots and thus further add to aeration and drainage.

The close correlation of root growth with soil temperature and moisture is very clearly seen. When moisture is plentiful, root growth varies as the soil temperature. While a little root growth may be found all through the winter when the bulk of the soil is at a temperature of 35° to 45° F., really active growth begins only when the soil temperature rises above 45° F. From 45° to about 69° F. (at 8 in. deep), the maximum reached under Malling conditions, root growth increases. This agrees remarkably well with the laboratory trials of Nightingale (9).

The exact degree of soil dryness which causes a check to root growth is less easy to define. There seems little doubt that dry soil conditions are largely responsible for the check in root growth noted in midsummer in this work. The soil moisture tension meters used seem to provide a reasonable scale of measurement for the soil dryness conditions, and by this scale a tension of 30 cm. to 40 cm. Hg was apparently sufficient to check root growth under Malling conditions. This is well below the wilting range. The check must therefore be due, not to the inadequate suction of the roots, which can exert one of many atmospheres (Ursprung and Blum (18)), but to the inadequate flow of water towards them through the soil as it becomes drier. The assigning of water shortage as the cause of the summer check agrees with the findings of Büsgen (2), Engler (5) and McDougall (8). Although his data also support this conclusion, Stevens (17) carefully omits to draw it because of the fact that relatively longer roots are usually found on relatively sandy soils. The explanation is surely that, while a small moisture gradient in the soil is certainly a stimulant to root growth, the optimum gradient is readily passed in midsummer, so that the root, with the heavy summer transpiration pull behind it, is unable to grow fast enough to keep up with its optimum moisture supply, and a check therefore results. The most stimulating gradient is probably quickly set up in sandy soils, and this, added to the easy growth conditions given by the sandy texture, results in increased growth for a limited time ; but beyond a certain limit, decreased water supply obviously checks growth. The matter clearly requires further study, but this explanation appears to fit the observed facts.

It seemed a little disappointing at first that the different rootstocks, so contrasting in their effect on growth and cropping, showed no dramatic contrasts in absorbing root type and conformation. A large difference in amount of root was, of course, visible, as was expected from other work (Rogers and Vyvyan (15)), but the most striking feature was the degree of similarity between the individual roots and between their reactions to physiological factors. The differences in period of growth and depth of root, though they may be important, became clear only when the records were finally summarized, and it is not possible to say definitely whether they are causes or results of rootstock effect. Other conclusions are given in the various sections and in the Summary.

ACKNOWLEDGMENTS.

In a research of this extent the help of many workers is needed, and the writer acknowledges with special gratitude the valuable assistance of Miss Beakbane and of many Recorders in drawing the roots and summarizing the results. His thanks are due to Dr. Hatton for advice and encouragement throughout, to Mr. R. C. Palmer for supervising the construction and installation

of the trenches from specifications and plans sent from Canada by the writer during his year's exchange visit to the Dominion Experimental Station, British Columbia, and to many others who gave advice and help in various ways.

IV. SUMMARY.

(1) Studies on the root growth of four fourteen-year-old Lane's Prince Albert apple trees on rootstocks E.M. I, IX and XVI, for four consecutive years, on deep sandy loam at East Malling, Kent, are described.

(2) The studies were made by means of special observation trenches provided with glass windows supported against the soil profile and normally protected from light.

(3) It was found possible to observe the position, time and rate of root growth, suberization and formation of laterals. The ultimate death and decay of some of the roots and secondary thickening of others was recorded. Root hairs and other features were observed with a binocular microscope ; and photographs, illustrating the root life history, were obtained.

(4) Soil temperature was recorded at two depths. Soil moisture was measured at two depths by means of moisture tension meters devised for the purpose.

(5) The growing apple roots were white and succulent, about 0·3 to 2 mm. diameter, bearing root hairs only 0·025 to 0·075 mm. long. The growth rate varied from nil to about 9·4 mm. per day ; 3 mm. per day was common during active growth periods.

(6) Suberization of the root usually occurred at the age of from a week to a month. The cortex then shrank and rotted away, leaving the central cylinder loose in its hole. Insects sometimes fed on the decaying roots, thus enlarging the passages, and aerating and cultivating the soil.

(7) The smaller roots usually died and disappeared. The larger ones usually persisted. Some developed relatively rapid secondary thickening, while others persisted without much swelling ; both types produced lateral roots.

(8) Root growth was closely correlated with soil temperature. Some growth, but very little, was found in winter, at soil temperatures from 35° to 45° F. Active growth began at temperatures from about 45° F. upwards, and increased with rising temperature up to the maximum recorded, about 69° F. (at 8 in. deep). Similarly, root growth decreased with falling temperature.

(9) A check in root growth under warm soil conditions usually coincided with drying of the soil, and a fresh spurt of root growth usually followed its remoistening, provided it was still warm. The degree of dryness at which a check to growth occurred usually corresponded to a soil moisture tension of

30 to 40 cm. Hg, but sometimes even lower tensions appeared to cause a check. Thus, soil moisture appears to act as a limiting factor to root growth well before the wilting range is reached.

(10) Soil moisture was usually plentiful from January to May, but from June or July until the onset of the autumn rains, the rainfall was often not enough to replace the water removed by the trees, and the soil steadily dried out.

(11) Root growth began before the leaves unfolded, and continued after shoot growth ceased. Relatively rapid root growth usually began in March or April, increased to a peak in June or July, and then fell off. A second peak sometimes occurred a month or so later, and a further small peak usually followed the onset of the autumn rains.

(12) The response of root growth to soil temperature and moisture can be seen locally as well as generally. Thus, the bulk of root growth is lower down or higher up according to seasonal soil conditions. In the spring, as the upper layers of soil warm up first, most growth occurs there ; in the winter, most root growth is in the lower layers.

(13) This work suggests that quick-acting fertilizers will be most effective if applied in early spring or early autumn, but that slower-acting manures can be utilized all the year round. Deep cultivation is likely to do more good and less harm if confined to the winter months.

(14) Many growing roots were seen below a depth of 40 in., but about twice as much root growth was noted between depths of 3 in. and 23 in. as between 23 in. and 43 in. Greatest root concentration was usually at a depth between 5 in. and 20 in.

(15) The growth of the roots of different rootstocks showed great contrasts in amount, following the above-ground vigour characteristics of the stocks. There was little difference in appearance between the individual absorbing roots. There were indications that the root growth of the most vigorous stock, No. XVI, differed from that of No. I and No. IX in the following ways: it reached its first peak more quickly, its general absorbing root distribution was rather deeper, and its suberization rate was very slightly slower. The mean growth rate per root was similar for all stocks, therefore the greater amount of root of No. XVI resulted from the possession of more, rather than of longer, absorbing roots.

(16) The methods of observation are described and criticized. The vertical position of the windows, and their division into $\frac{1}{2}$-in. squares, by which root growth can accurately be charted, appear to give better results over long periods than previously employed methods.

Observation trenches of the kind described appear to have further wide possibilities for many types of root study under field conditions.

REFERENCES.

(1) *Aaltonen, V. T.* Über die Ausbreitung und der Reichtum der Baumwurzeln in den Heidewäldern Lapplands. Acta Forrestalia Fennica, 1920, **14**, 1.

(2) *Busgen, M.* Einiges über Gestalt und Wachstumsweise der Baumwurzeln. Allgemeine Forst- und Jagd-Zeitung., 1901, **77**, 273, 303.

(3) *Cannon, W. A.* and *Free, E. E.* Physiological features of roots with special reference to the relation of roots to aeration of the soil. Carnegie Inst. Pub. 368, 1925.

(4) *Conrad, J. P.* and *Veihmeyer, F. J.* Root development and soil moisture. Hilgardia, 1929, **4**, 113.

(5) *Engler, A.* Untersuchungen über das Wurzelwachstum der Holzarten. Mitt. Schweiz. Zentralanst, forst. Versuchsw., 1918, **7**, 247.

(6) *Haasis, F. W.* Relations between soil type and root form of western yellow pine seedlings. Ecology, 1921, **2**, 292.

(7) *Heinecke. A. J.* The effect of submerging the roots of apple trees at different seasons of the year. Proc. Am. Soc. Hort. Sci., 1933, **29**, 205.

(8) *McDougall, W. B.* The root growth of forest trees. Amer. Journ. Bot., 1916, **3**, 384.

(9) *Nightingale, G. T.* Effects of temperature on growth, anatomy and metabolism of apple and peach roots. Bot. Gaz., 1935, **96**, 581.

(10) *Rogers, W. S.* Root studies IV: A method of observing root growth in the field; illustrated by observations in an irrigated apple orchard in British Columbia. East Malling Res. Sta. Ann. Rep. for 1933 (1934), 86.

(11) ———. A soil moisture meter depending on the "Capillary Pull" of the soil, with illustrations of its use in fallow land, grass orchards and irrigated orchards. Journ. Agric. Sci., 1935, **25**, 326.

(12) ———. The relation of soil moisture to plant growth, illustrated by moisture meter experiments with strawberries. East Malling Res. Sta. Ann. Rep. for 1935 (1936), 111.

(13) ———. Soil moisture studies I. Water utilization by apple trees in cultivated and grass orchards compared with fallow land. East Malling Res. Sta. Ann. Rep. for 1936 (1937), 105.

(14) ———. Root studies VII. A survey of literature on root growth, with special reference to hardy fruit plants. Journ. Pom. & Hort. Sci., 1939, **17**, 67.

(15) *Rogers, W. S.* and *Vyvyan, M. C.* Root studies V. Rootstock and soil effect on apple root systems. Journ. Pom. & Hort. Sci., 1934, **12**, 110.

(16) *Scott, L. I.* and *Priestley, J. H.* The root as an absorbing organ, I and II. A reconsideration of the entry of water and salts in the absorbing region. New Phytologist, 1928, **27**, 125.

(17) *Stevens, C. L.* Root growth of white pine. Pinus Strobus L. Yale Univ. Sch. of Forestry Bull. 32, 1931.

(18) *Ursprung, A.* and *Blum, G.* Zur Kenntniss der Saugkraft V. Ber. deut. Bot. Ges., 1921, **39**, 139.

(19) *Veihmeyer, F. J.* Some factors affecting the irrigation requirements of deciduous orchards. Hilgardia, 1927, **2**, 125.

(20) *Von Alten, H.* Wurzelstudien. Botanische Zeitung, 1909, **67**, 175.

(*Received* 22/12/38.)

FIG. 1.

General view of root observation trench (Series D), installed beside Lane's Prince Albert apple on rootstock No. XVI. Two observation windows are shown uncovered. A thermograph and a recording soil moisture meter are seen on the left.

FIG. 2.

Apparatus for taking photomicrographs arranged in observation trench C. Another uncovered window and the record board used for the root plans can also be seen to the left.

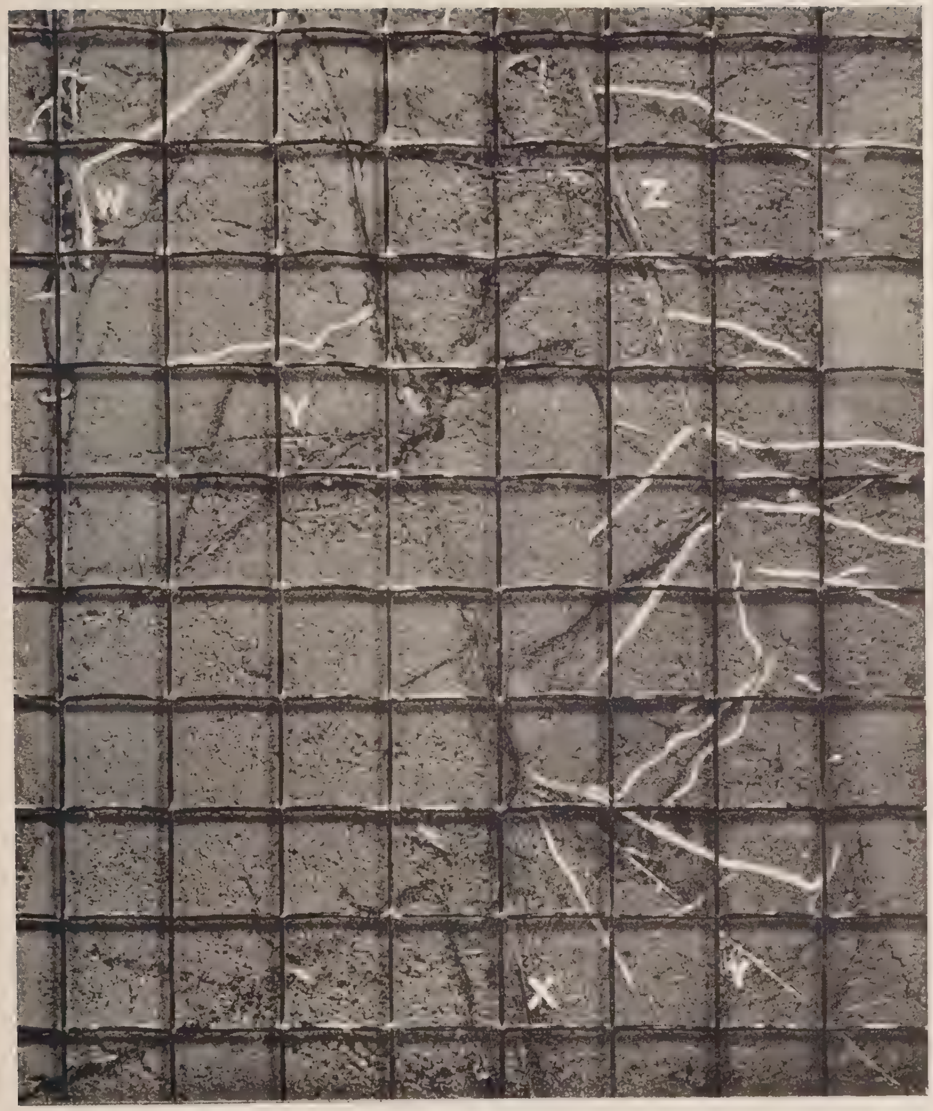


FIG. 3.

Growing roots of Lane's Prince Albert apple on stock No. XVI, in June, 1937. Besides the new white roots, older suberized roots just sloughing off their cortex (X), roots of which only the central cylinder remains (Y) and roots which have developed secondary thickening (Z) can be seen. At (W) a root has reached a worm hole and begun to grow down it. The wires embedded in the glass form ½-in. squares. (Magnification 1·2.)

FIG. 4.

Photomicrograph of apple rootlet (rootstock No. I) growing in observation trench, July 19th, 1933. Note (A) root cap, (B) elongating region, (C) young root hairs, (C1) Older root hairs. (Magnification about 4·8.)

FIG. 5.

The same root 2 days later. It had grown 6 mm. in length.

PLATE V.

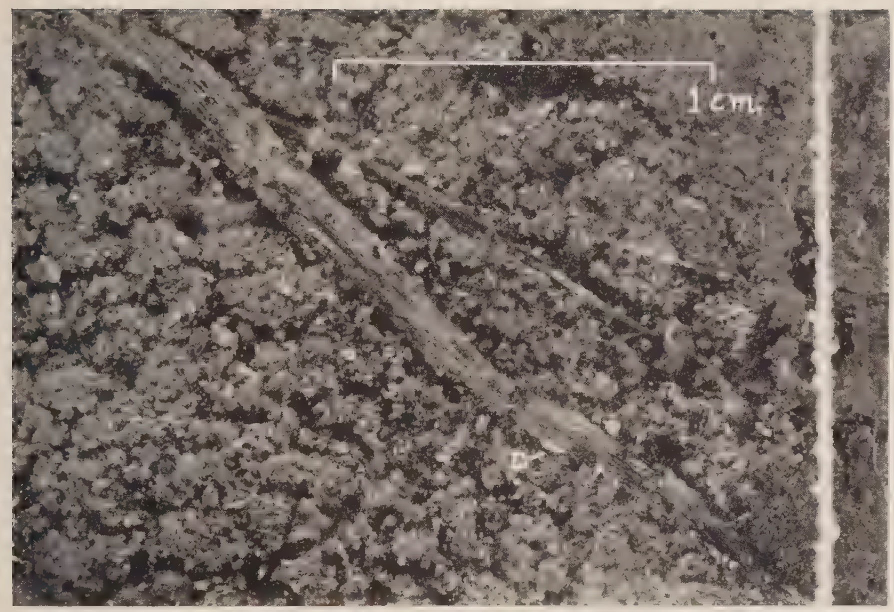


FIG. 6.

The same root 24 days later, August 4th. Note brown suberized and shrivelling cortex. A Collembolon larva (D) is seen eating the cortex.

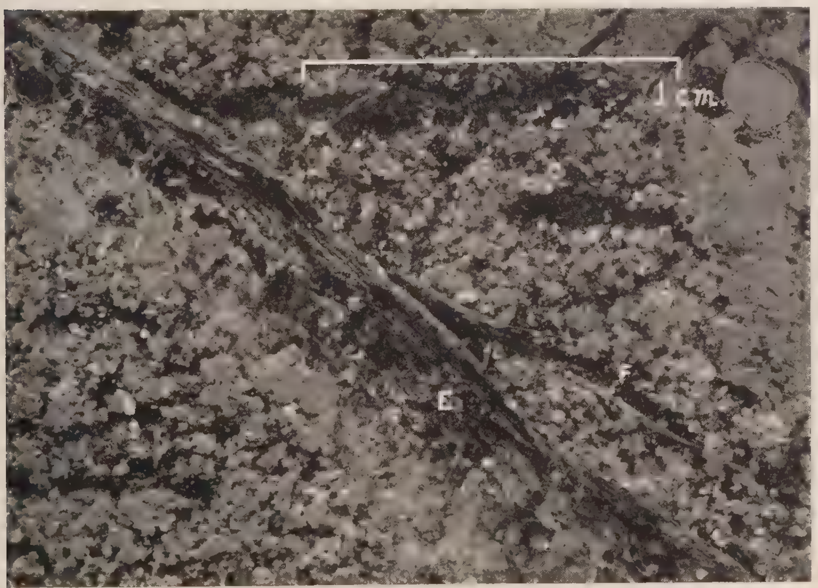
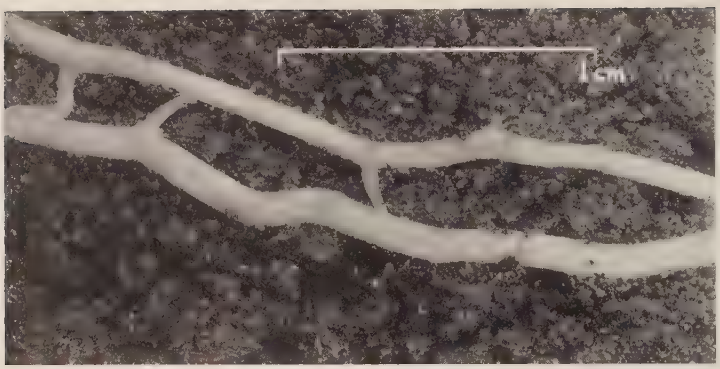
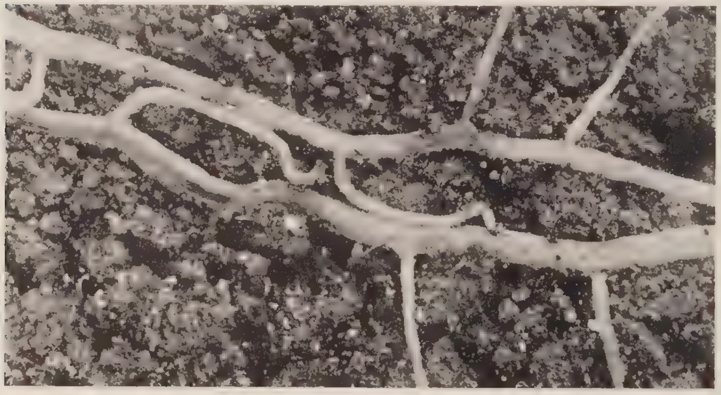


FIG. 7.

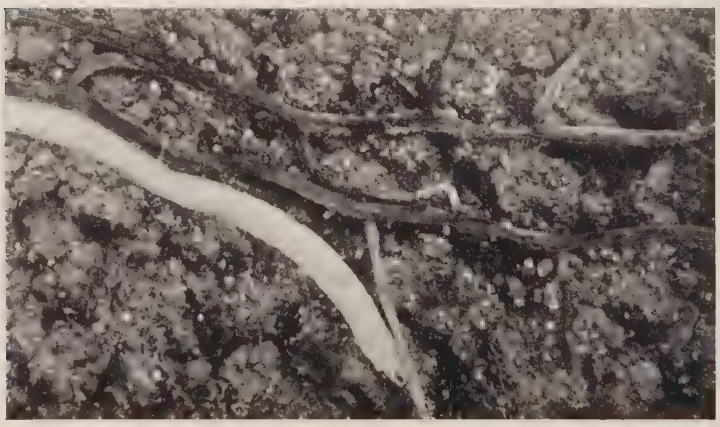
The same root 78 days later, October 31st. Further rotting of cortex. Central cylinder beginning to be exposed (E) and worm burrow (F) made along hole left by shrinking root.



(a). Photomicrograph of apple roots on July 18th, 1931. The two large roots grew between July 10th and 16th. Small laterals are seen emerging. (Magnification about 4·4.)



(b). The same roots 19 days later, August 5th. Suberization beginning.



(c). A further 29 days later, September 3rd. Original roots completely brown. A new root has grown along one of the shrinking old roots.

FIG. 8.

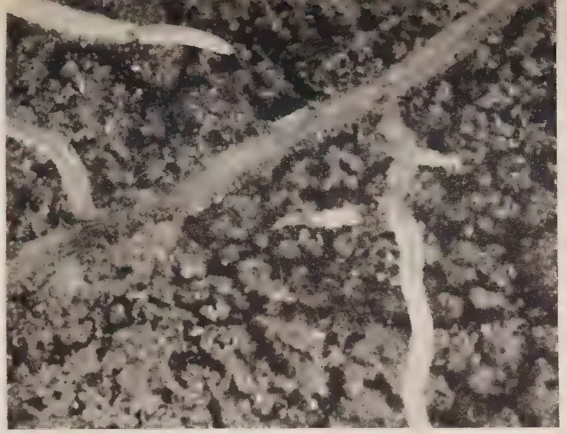


Fig. 9.

Photomicrograph showing three orders of apple roots. 1st order recorded June 17th, 2nd order July 2nd, 3rd order July 7th. (Magnification 3·3.) Photo taken July 11th.

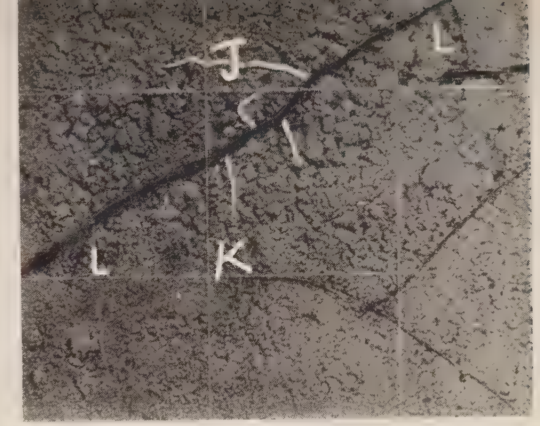


Fig. 10.

Laterals growing in June, 1932, from a root formed September 31st. Dying laterals of 1931 (L L) can also be seen. The marking is in 1-in. squares in this case. (Natural size.)

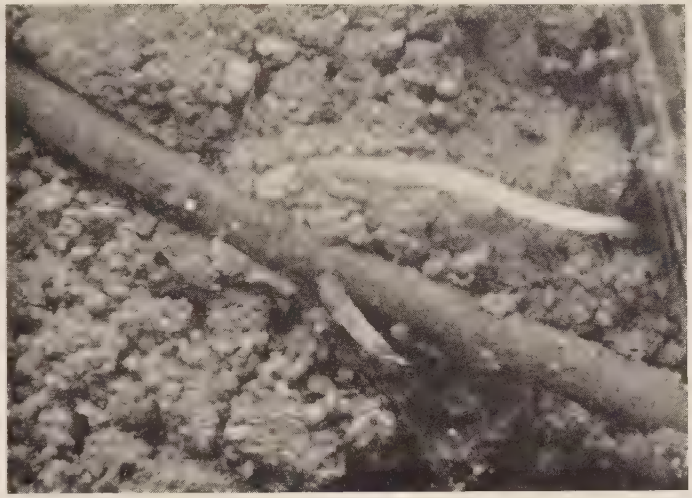


Fig. 11.

Laterals growing from a 6-year-old root. Note the translucent nature of the lower lateral. (Magnification 6·6.)

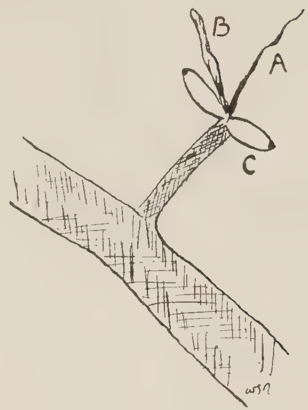


Fig. 12.

Diagram showing production of new laterals from stump of an old lateral. A—rotting end. B—suberizing sub-lateral. C—new sub-laterals. (Magnification about 3.)

Fig. 13.

Growing tip of root of rootstock No. XVI, showing root cap (A), young root hairs (C) and older root hairs with drops of exudate (C1). The elongating region is partly hidden by the wire in the glass. (Magnification about 12·6.)

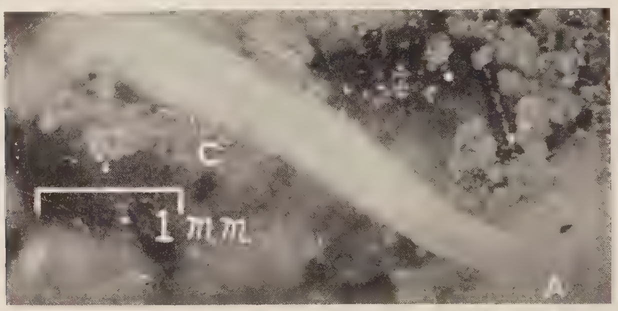


Fig. 14.

Small growing tip of root of rootstock No. I, showing root cap (A) and root hairs with small globules of exudate (C). (Magnification about 20.)

ROOT STUDIES

IX. THE EFFECT OF LIGHT ON GROWING APPLE ROOTS: A TRIAL WITH ROOT OBSERVATION BOXES

By W. S. ROGERS
East Malling Research Station

In a previously reported experiment with root observation trenches (3) provided with plate-glass windows, installed beside mature apple trees in the orchard, the roots, though normally covered by light-proof shutters, were exposed to daylight during the recording periods. Since such exposure is obviously abnormal for growing roots, two simple trials were carried out to determine its effect. For convenience and economy these were carried out with young apple stocks in small observation boxes, the general appearance of which is shown in Fig. 1, Plate I.

The boxes were placed on strong wooden trestles 32 in. high, which brought the windows up to a convenient height for observing and recording the behaviour of the roots. The soil in the boxes was, of course, exposed to greater temperature fluctuations than occur in a normal orchard. These can be lessened by sinking the boxes into holes in the ground, and hoisting them up for observation, and this was tried in a previous experiment (unpublished), but was found very laborious. In any case, the temperature fluctuations for the boxes on trestles are at least the same for all the boxes, and their main effect is probably to emphasize the normal seasonal effects.

Artificial watering was necessary, as in all pot trials. It was not difficult to keep the moisture conditions uniform at a high level, by reasonably frequent saturation of the boxes and allowing the surplus to drain away. If comparable drier conditions are wanted, the use of soil moisture tensiometers in each box would be desirable, so that the soil could be re-saturated when it reached a pre-determined moisture tension (2).

The same boxes have been used with success for some strawberry root observations (unpublished) and for observations on the root growth of compatible and incompatible stock:scion combinations, recently described by Chang (1). The design and arrangement has, in fact, proved very satisfactory for observing and comparing the effect of various treatments on the roots of small plants for one or two years, under conditions which, though definitely not natural, can be fairly closely controlled.

Construction of Observation Boxes.

The boxes were strongly constructed of wood, and were 24 in. long, 17 in. high and 7 in. wide (inside measurements). Vertical plate-glass windows,

$23\frac{1}{2}$ in. × 15 in., reinforced with wires forming $\frac{1}{2}$-in. squares,* were fitted to the two large sides, resting on rubber strips $\frac{1}{8}$-in. thick, on wooden fillets. In the later experiments the windows were sloped $\frac{3}{4}$ in. inwards towards the bottom, as this overcame a slight tendency for the soil to shrink away from the glass as it dried. The windows were normally covered with detachable wooden shutters having double light-traps at the edges. The dimensions and construction can be seen from Fig. 2.

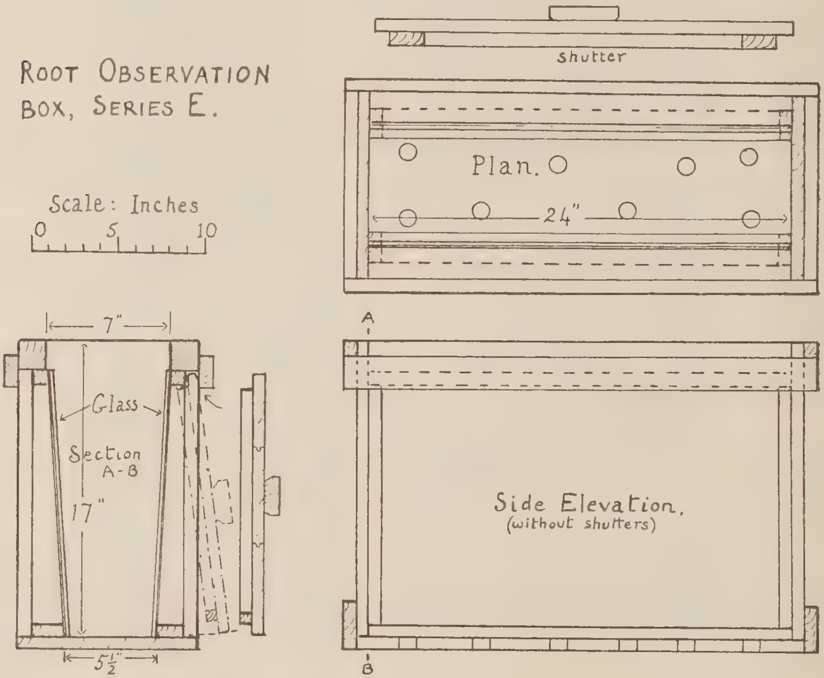


Fig. 2.—Scale Plans of root observation box.

The boxes were well painted with black bitumastic paint inside, to resist rotting, and with white lead paint outside to reflect the sunlight and so avoid excessive heating. The shutters were black round the light-traps, to avoid the entrance of reflected light. The boxes were filled with loam which had been sterilized to avoid fouling of the glass by worms and soil insects. Each box held about 120 lb. of dry soil. The trees, the roots of which it was proposed to observe, were planted equidistant from the two windows, and the soil was well soaked with water. Good drainage holes had been made in the bottoms of the boxes, and a layer of crocks covered the holes.

* This was " Pilkington's wired Georgian plate ". For photographic work plain $\frac{1}{4}$ in. plate-glass is better, however, and squares may be marked on the inner side, with a writing diamond, before installation.

TRIAL I.

Six boxes were used, each containing three unworked one-year-old No. I rootstocks, planted in April 1933. The following treatments were given:—

(1) Always uncovered.

(2) Exposed for twenty minutes three times a week.

(3) Exposed for two hours once a fortnight.

(4) Total darkness.

One window in each box had treatment 4, i.e. the shutter was not opened until August 18th. The other windows had the three other treatments, each occurring in two boxes, arranged as shown in Fig. 3. The boxes were placed

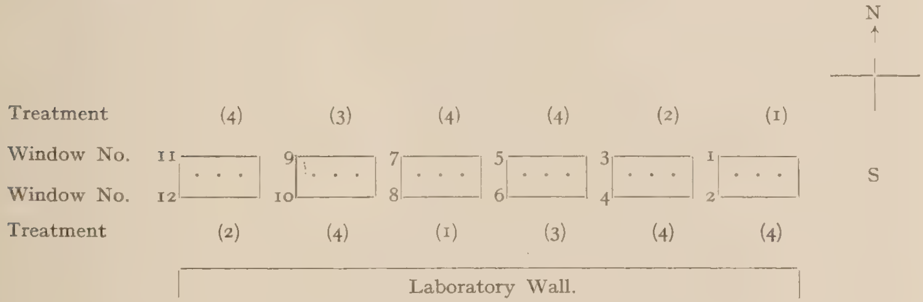


Fig. 3.—Arrangement of boxes in Light Trial I.

Treatments (1) Always uncovered.
(2) Exposed for 20 minutes 3 times a week.
(3) Exposed for 2 hours once a fortnight.
(4) Total darkness.

on the north side of a laboratory building, the shade of which prevented direct sunlight from reaching the windows. The treatments were arranged to occur equally on the north and south sides of the boxes, but otherwise were randomized.

Results.

The behaviour of the roots in treatments 1, 2 and 3 was recorded at fortnightly intervals. A few roots were noted on June 9th and 23rd, but it was not till July 7th that roots were seen at all of the windows under these treatments, and on this date the exposure treatments were started. The roots that were constantly exposed to light continued to grow actively, but by July 10th many of their tips were bright red, as compared with the normal grey. Parts of the normally white rootlets also showed a pink coloration (but not on the root hairs). New roots kept coming to the glass, however, and apparently there was no marked negatively heliotropic response, for roots growing along the glass did not turn away any more consistently or rapidly than they do in complete

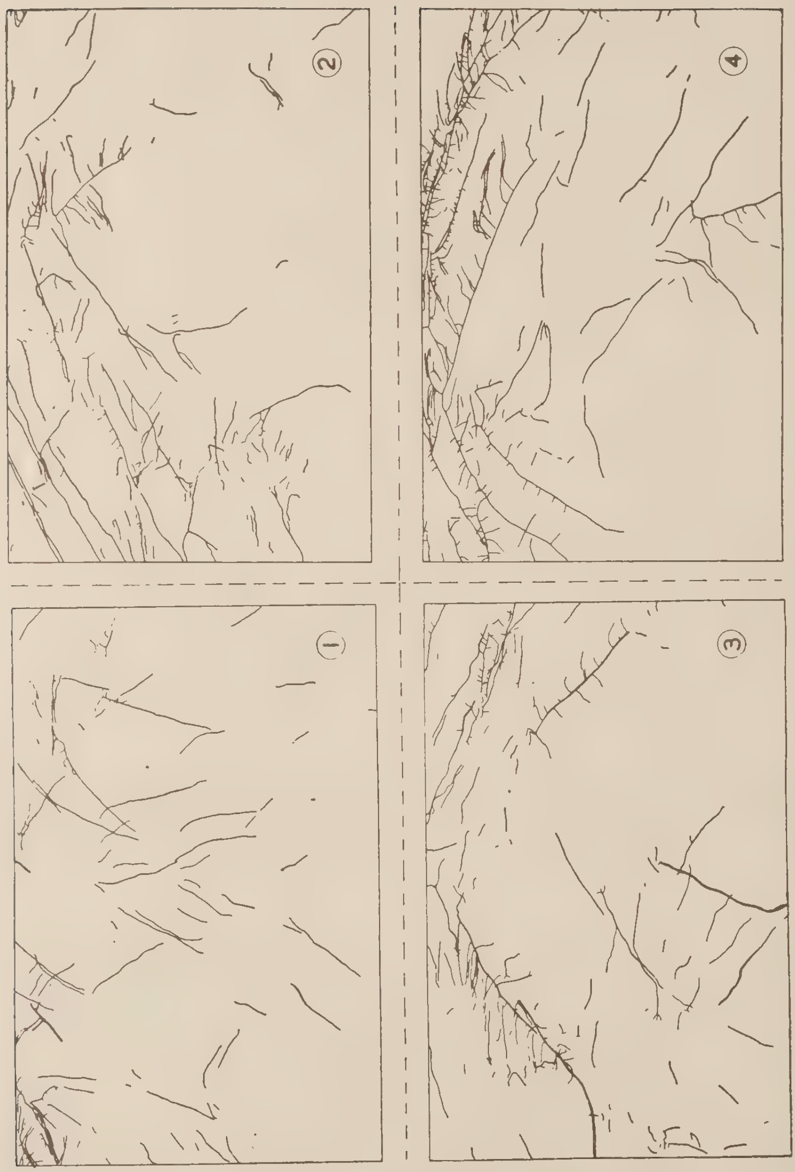


FIG. 4.

Light trial I. Typical plans of root growth to end of season. (1) Always uncovered. (2) Exposed for 20 minutes three times a week. (3) Exposed for two hours once a fortnight. (4) Total darkness.

darkness. The growth of roots continuously exposed was nevertheless severely checked, and at the final count their numbers fell well below those at other windows. This was chiefly due to the marked lack of development of small lateral roots from the exposed main roots. The comparison of numbers is not exact, since the totals of the various exposed treatments are obtained by adding together the numbers of growing roots at each fortnightly recording, while those of the covered windows are the numbers of growing and also of suberized roots observed at the final opening. Probably the best comparison is given by the plans of the roots themselves. The root growth at typical windows by the end of the season can be seen in Fig. 4. Window 1 shows the sparse main roots with practically no laterals seen on the constantly exposed windows. Window 4, constantly covered until records of the roots were made at the end of the first part of the experiment, shows the larger number and greater growth of roots, with many more laterals, obtained in total darkness. Windows 2 and 3, exposed to light for twenty minutes three times a week, and two hours once a fortnight, respectively, show some checking, especially of the laterals, but are not very unlike the dark windows. Windows 2 and 4 were on opposite sides of the same box.

The figures for root growth in each box until August 18th, when the first part of the experiment was ended, and for the further period to October 9th, are given in Table I. Each exposed window is compared with its own control (covered) window, on which the whole growth was recorded on August 18th and October 9th. This tends to cut out variation due to differences in branch growth, but even so it is seen that great variation occurred within each treatment. Window E9, exposed for two hours once a fortnight, had much more growth than any other window, whether covered or exposed. It is clear, however, that continuous exposure to light cuts down the number of roots and total growth by about 50%, while exposure for two hours in a fortnight, both in twenty minute periods and in a single period, tends to check growth much less severely. The single period is probably less detrimental, for the roots then have a continuous fortnight in the dark. Further analysis of the records (not given here) shows that the check is recognizable both in mains and laterals, but is greatest in the latter.

Suberization.

The total length of white unsuberized root was recorded each fortnight, as well as the length of new growth. By dividing the unsuberized root length by the new growth length over a relatively long period a rough measure of the mean time taken for a root to suberize is obtained. This method has been discussed more fully in the previous paper (3). The mean suberizing period calculated in this way was 7·3 days in the fully exposed windows, 12·1 days in those having

TABLE I.

Effect of Light on Root Growth. Trial I. (Lengths in 1/10 in.)

Window No.	Treatment.	1st Period: to August 18th. Root Growth. No.	Length.	Average length.	Percentage difference. No.	Length.	Average length.	2nd Period: August 19th-September 29th. Root Growth. No.	Length.	Average length.	Percentage difference. No.	Length.	Average length.
E1	(1) Always exposed ..	148	786	5·3	−38	−54	−24	67	825	12·3	−25	−18	+ 9
E2	(4) Always covered ..	245	1710	7·0				89	1005	11·3			
E8	(1) Always exposed ..	121	827	6·8	−73	−69	+11	74	626	8·5	+ 1	+ 3	+ 2
E7	(4) Always covered ..	443	2649	6·0				73	608	8·3			
	Mean				−56	−62	− 7				−12	− 8	+ 6
E3	(2) Exposed for 20 minutes three times a week ..	237	1262	5·3	−21	−39	−15	84	738	8·8	+83	+ 9	−41
E4	(4) Always covered ..	334	2067	6·2				46	679	14·8			
E12	(2) Exposed for 20 minutes three times a week ..	342	1852	5·4	+11	−26	−33	92	768	8·3	+113	+49	−31
E11	(4) Always covered ..	307	2491	8·1				43	517	12·0			
	Mean				− 5	−33	−24				+98	+29	−36
E6	(3) Exposed for 2 hours once a fortnight ..	236	1300	5·5	−14	−25	− 8	96	709	7·4	+66	+18	−29
E5	(4) Covered	286	1728	6·0				58	601	10·4			
E9	(3) Exposed for 2 hours once a fortnight ..	547	3095	5·7	+168	+116	−19	66	394	6·0	+247	+42	−59
E10	(4) Covered	204	1433	7·0				19	278	14·6			
	Mean				+77	+46	−14				+156	+30	−44

twenty minutes three times a week, and 11·9 days in those having two hours once a fortnight. In the same period two windows of Trench C (No. I rootstock) in the previously mentioned field trials, observed *monthly*, showed a mean suberizing period of 18·6 days. These windows actually underwent two periods of exposure, of twenty and twenty-four minutes respectively. During each month many new roots had grown and suberized in complete darkness. Two other windows, which had only five minutes exposure (as the roots were fewer in number) actually showed rather more rapid suberization. It is therefore probable that the suberization figure given by monthly observations is not far from that of continuous darkness (which is not, of course, directly obtainable). It is clear that above a certain value, greater exposure to light causes more rapid suberization, but it is likely that the ten to fifteen minutes usually spent at each window in the field observation trenches in taking the weekly records (3) does not very greatly affect the results. In the peak periods of growth, however, over an hour was sometimes spent on a single window, and this probably increased both the check and suberization. This would therefore tend to *decrease* the contrasts in growth shown in the graphs of seasonal growth discussed in the previous paper (3), and as marked contrasts were nevertheless seen, their validity is, if anything, greater than it appears.

Trial I was continued for a second period, August 18th to September 29th, during which the growth of the roots at all windows was more even. In most cases there was actually less root at the completely covered windows than at the exposed ones. Probably root competition was beginning to have a marked effect, and, of course, the days were getting shorter.

TRIAL II.

In 1934 four boxes were used in a simpler trial. One window of each box was exposed for thirty minutes weekly, and the other was kept uncovered. The same boxes and soil were used, but instead of No. I rootstock, two No. II rootstocks were planted in the middle. It was thought that the behaviour of these, being more sparsely rooting than No. I, might be easier to record. No. II was not used in the field observation trench trials. Actually, a greater number of roots per window was finally recorded, but their total length was less. The results are shown in Table II. At the end of the first period, on August 18th, the mean difference between the exposed and covered windows was: Number, -1%; total length, -46%; mean length, -45%. In the second period, ending October 3rd, the differences were again less, being: Number, $+2\%$; total length, -34%; mean length, -29%.

The results from the four replicates in Trial II were subjected to statistical analysis, which showed that the reduction in mean length per root in the exposed series was statistically significant in the first period. The differences in number

TABLE II.

Effect of Light on Root Growth. Trial II. (Lengths in 1/10 in.)

Window No.	Treatment.	1st Period: to August 8th. Root Growth. No.	Length.	Average length.	Percentage difference. No.	Length.	Average length.	2nd Period: August 9th-October 3rd. Root growth. No.	Length.	Average length.	Percentage difference. No.	Length.	Average length.
F5A	Exposed	280	667	2·4	− 3	−43	−40	99	188	1·9	−44	−73	−51
F5B	Covered	288	1161	4·0				178	700	3·9			
F6B	Exposed	438	1089	2·5		−44	−43	276	627	2·3	+55	−14	−44
F6A	Covered	439	1955	4·4				178	732	4·1			
F7B	Exposed	402	1211	3·0	−38	−67	−47	190	565	3·0	−44	−59	0
F7A	Covered ..	649	3693	5·7				457	1368	3·0			
F8A	Exposed	452	1471	3·3	+36	−31	−48	220	716	3·3	+41	+ 9	−21
F8B	Covered	333	2143	6·4				156	652	4·2			
	Mean				− 1	−46	−45				+ 2	−34	−29

and in length of roots were not significant in either period ; and in the second period the difference in mean length was also not significant. Trial II therefore confirmed the general conclusions from Trial I that prolonged exposure of roots to light in the periods of greatest light intensity checks growth, but with less light the check becomes insignificant.

Two other tests were made in the observation trenches themselves. Certain shutters in the trenches were kept closed for a whole season. On opening them at the end of it, the root growth did not look markedly different from that at the windows opened for recording purposes weekly. The lateral growth appeared a little longer, however. In another series, the behaviour of the roots of No. IX at one pair of windows was recorded first by yellow and later by red light from an electric hand lamp (the trench being kept dark by closing the roof). This proved an unsatisfactory method, as the light intensity was too low to show the roots properly, and suberization could not be seen readily. No appreciable difference in growth was noted, but this may have been because growth was very slight at these windows in any case. If recording by artificial light proved to have no checking effect on the roots, and a main electricity supply could be brought to the trenches, this might be more satisfactory than observation by diffused daylight ; but daylight appears quite satisfactory for many purposes, and the increase in detail of observation obtainable probably compensates for the loss of information due to the check caused by the light.

SUMMARY.

(1) Two trials of the effect of exposure of growing apple roots to daylight were carried out with unworked rootstocks, Malling Nos. I and II, in small root observation boxes. The main object was to determine the effect of exposure of apple roots to light during recording periods, in some field trials with root observation trenches previously described. In all cases the roots were shielded from direct sunlight.

(2) No marked negatively heliotropic response was found. Continuous exposure to daylight severely checked root growth, hastened suberization and checked the development of lateral roots. Exposure for periods of twenty minutes to two hours caused some, but much less check. The reduction in length of root caused by weekly exposure for thirty minutes was statistically significant in the early summer, when light intensity was high, but not significant in late summer and autumn.

(3) It is concluded that the amount of checking of root in the previous trial, in the short periods of exposure necessary for recording, is not of very great importance. In any case, the check is greatest at the periods of greatest root growth so that its effect is to lessen the contrasts in growth between different

periods. As these contrasts were nevertheless very marked, their validity is, if anything, greater than it appears.

(4) Small observation boxes, mounted on trestles, are described. They appear very suitable for the comparison of certain treatments on the roots of small plants for one or two years. Scale drawings are given.

REFERENCES.

(1) *Chang, W. T.* Studies in incompatibility between stock and scion. Journ. Pom. & Hort. Sci., 1938, **15**, 267.

(2) *Rogers, W. S.* The relation of soil moisture to plant growth, illustrated by moisture meter experiments with strawberries. East Malling Res. Sta. Ann. Rept. for 1935 (1936), 111.

(3) ———. Root studies. VIII. Apple root growth in relation to rootstock, soil, seasonal and climatic factors. Journ. Pom. & Hort. Sci., 1939, **17**, 99.

(*Received* 22/12/38.)

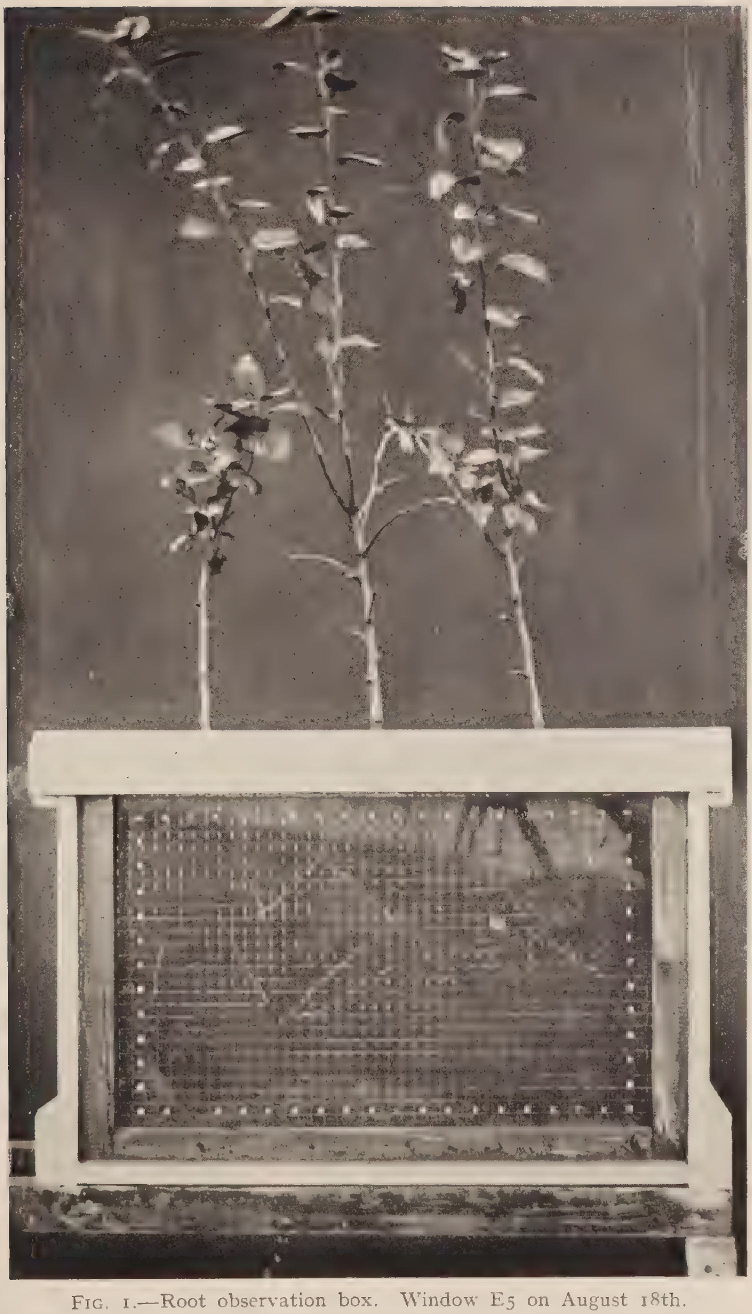


Fig. 1.—Root observation box. Window E5 on August 18th.

ANATOMICAL STUDIES OF STEMS AND ROOTS OF HARDY FRUIT TREES

II. THE INTERNAL STRUCTURE OF THE ROOTS OF SOME VIGOROUS AND SOME DWARFING APPLE ROOTSTOCKS, AND THE CORRELATION OF STRUCTURE WITH VIGOUR

By A. BERYL BEAKBANE and ELEANOR C. THOMPSON
East Malling Research Station

FOR many years, workers who have handled apple rootstocks have realized that they differ in certain characteristics connected with their internal structure, such as the thickness of the bark and the brittleness of the stem and root. In 1936, Beakbane and Renwick described the anatomy of the roots of the East Malling No. IX apple rootstock worked with a number of different scion varieties (1). They found that the roots of No. IX had a structure which differed greatly from that of the roots of most of the scions, and that although the structure of No. IX varied a little when worked with these different scions, on the whole it remained remarkably constant. Roots of No. IX grown on another soil and from trees of a different age were found to resemble those from the main series very closely. Observations had also been made on the structure of the rootstocks Nos. II and XII. These differed considerably from each other and from No. IX, No. II being intermediate in structure between Nos. IX and XII.

From these preliminary observations it was decided that an examination of the structure of a series of rootstocks showing a wide range of vigour would be of value in order to discover whether any correlation existed between the internal structure of a rootstock and the degree of vigour which that rootstock would impart to a scion variety. Suitable material for such a study was available from a series of four-year-old trees of Lane's Prince Albert, budded on Malling Nos. VII and IX and on eight new clonal rootstocks, showing a wide range in vigour. These new clonal rootstocks had been selected after propagation tests from seedlings raised by Mr. M. B. Crane at the John Innes Horticultural Institution, by crossing two dwarfing rootstocks, No. VIII (French Paradise) and No. IX (Jaune de Metz). It was hoped that some new semi-dwarfing, as well as dwarfing, rootstocks would be found among these seedlings, and for this reason No. VII was included as a standard semi-dwarfing, and No. IX as a dwarfing, rootstock. As no trees on No. VIII had been included in this series, roots were examined from older trees of Lane's Prince Albert on

No. VIII, grown on the same type of soil, so that a comparison could be made between the structure of both parents, Nos. VIII and IX, and of the seedlings from the cross.

The vigour, cropping, disease resistance and morphological characteristics of the root systems of Lane's Prince Albert trees worked on the rootstocks described above has been fully reported by Tydeman (3, 4 and 5). The trees were grown at 2 to 2½ ft. apart, in rows 5 ft. 6 in. wide, in the intensive type of nursery trial described by Tydeman (5). The rootstocks were budded *in situ*, and the trees were allowed to grow naturally with very little pruning.

Method of Examination.

Observations were made on the internal structure of the roots of eighty-six trees. Three-year-old roots from ¼-½ in. in diameter were chosen from within a radius of 1 ft. 6 in. from the stock stem. Transverse sections of the roots of at least six trees on each rootstock were cut, stained with safranin and light green, and mounted in Canada balsam. The width of the bark and the diameter of the wood cylinder of the roots of all six trees were measured. Sections of the roots of three trees were chosen for examination of the wood in greater detail. On each of these sections, three "fields" between 345 and 690μ from the cambium, and spaced as evenly as possible within this band of xylem, were examined by means of a projection apparatus. A photograph of each "field" was obtained by projecting the image upon bromide paper, which yielded a photo-micrographic negative print with a magnification of 550 diameters. Similar photo-micrographs, but of lower magnification, are reproduced in Figs. 1 to 8. From these photo-micrographs, studies were made of (i) the relative area occupied by the four elements, fibres, parenchyma, vessels and rays composing the wood, (ii) the relative area occupied by living as compared with dead tissue, (iii) the number and (iv) the size of each of the four elements present.

(i) *The Relative Area of Bark to Wood.*

From transverse sections of the roots of six trees on each rootstock, measurements of the wood and of the bark (i.e. all tissues outside the cambium)* were made with a micrometer. The measurements were made across each section in two directions as nearly as possible at right angles to each other. Two measurements of the diameter of the wood, and four of the width of the bark, were obtained in this way, and the approximate areas of the wood and of the band of bark were calculated. A very clear negative correlation was found to exist between the bark: wood ratio and the vigour of the scion, as can be

* The interpretation of the terms used in this paper are those given in the "Glossary of Terms used in Describing Woods", published by the Committee on Nomenclature of the International Association of Wood Anatomists (6).

seen from Table I. In this table the rootstocks Nos. VII and IX are given in Roman, and the new clonal rootstocks in Arabic figures. The rootstocks are arranged in order of the bark : wood ratio in column one of the table, and in descending order of vigour of scion (as shown by four years' wood growth) in column three. The wood growth is the mean of measurements of twenty trees on each rootstock. The wood growth of trees on No. VII should be considerably higher (approximately 50 metres) than it appears in Table I, since the growth of the trees in one of the four blocks in the nursery trial was only about one-third that of those in the other three blocks. As the trees appeared to be healthy, although dwarfed, they have been included in the analysis. It is probable, however, that they are not typical and that the dwarfing may have been due to

TABLE I.

Correlation between bark : wood ratio and vigour.

Bark : Wood.		Vigour.	
Rootstock No.	Ratio.	Rootstock No.	4 years' wood growth. m.
45	0·61	128	53·9
128	0·71	45	53·3
125	0·73	125	50·6
VII	0·91	VII	43·2
90	0·98	90	36·7
108	1·04	9	32·2
9	1·55	IX	30·5
IX	1·82	108	29·7
29	1·93	29	21·5
99	2·29	99	16·0
Sig. diff. (p. =0·5)*	*0·30*		*10·0*

* Probability, (p) = ·05, shows that the odds are 20 to 1 against the significant differences shown being due to chance.

severe root competition from a neighbouring nursery row of young cherries, for a considerable number of cherry suckers were found among the trees in this block. It should be noted that although No. VII rootstock imparts very vigorous growth to the scion in the early years, in older trials it has been found that growth falls off as the tree comes into cropping at about eight years old (2).

It is interesting to note that the wood measurements of the roots of a series of nine-year-old Lane's Prince Albert trees on rootstocks Nos. 45, 125, 9, IX, 108 and 29 show that the order of vigour is very similar to that found after four years' growth in the present series.

The general similarity in the order of the rootstocks in columns one and three of Table I is so great that no description of the table is required. No. 108 is the only exception, with a bark : wood ratio of 1·04, although it has proved to be a moderately dwarfing rootstock.

(ii) *Relative Areas of Fibres, Parenchyma, Vessels and Rays in the Wood.*

The photo-micrographs described above were cut up into the four elements present in the wood and weighed in the following groups: (1) fibres, (2) parenchyma, (3) vessels and (4) rays, and the percentage areas were estimated by the method described by Beakbane and Renwick (1). These are set out in Table II. The relative areas occupied by fibres, vessels and rays all showed considerable variation from one rootstock to another, but the percentage of parenchyma varied comparatively little. It is interesting to note that in the high proportion of rays and low proportion of fibres and vessels, the structure of No. IX is very similar to that previously found by Beakbane and Renwick

TABLE II.

Percentage area of fibres, parenchyma, vessels and rays in the wood; mean wood growth and mean fruit buds per metre wood growth.

Root-stock No.	4 years' wood growth m.	Fibres. %	Paren-chyma. %	Vessels. %	Rays. %	Mean No. fruit buds per m. wood growth.
128	53·9	32·0	29·0	13·1	26·0	1·6
45	53·3	27·0	28·8	21·9	22·3	2·1
125	50·6	34·1	30·6	11·7	23·6	1·3
VII	43·2	34·5	24·2	16·5	24·8	1·6
90	36·7	20·2	31·2	10·4	38·2	2·8
9	32·2	25·0	32·4	7·7	34·8	3·8
IX	30·5	18·4	34·8	6·5	40·4	5·1
108	29·7	16·5	30·4	6·4	46·7	4·4
29	21·5	23·6	31·8	8·2	36·4	6·4
99	16·0	18·3	30·0	4·9	46·8	7·8
VIII*	—	22·7	23·4	15·7	38·2	—

* These figures are not strictly comparable with the main series; see text, p. 141.

in trees of No. IX worked with the same scion variety, though grown under very different conditions (1). No. VII, which had not been examined previously, had a greater area of vessels, nearly twice the percentage of fibres and a much smaller area of ray tissue than No. IX.

Although sections of No. VIII were taken from trees which were not strictly comparable with the main series, photo-micrographs were made, cut up and examined in the same way as for the other trees, and the relative area of the four elements of the wood calculated. The percentage of rays and fibres was approximately the same as in No. IX, but the percentage of parenchyma was lower, and of vessels much higher, than in No. IX. A photo-micrograph showing the structure of No. VIII is reproduced in Fig. 6.

The average number of fruit buds per tree, relative to size, over a four-year period showed that there is a marked negative correlation between vigour

and precocity up to this age; and, since the internal structure of the root appears to be associated with vigour, it is associated also with fruit bud formation. The only exception is No. 45 which, in spite of having the lowest percentage of ray tissue, was found to have the greatest number of fruit buds per metre wood growth among the four vigorous rootstocks. No. 45, however, had a lower percentage of fibres than Nos. 128, 125 and VII, and in this way resembled the more dwarfing rootstocks.

The association between vigour of scion and the proportion of the different elements present in the wood is further illustrated in Table III, where the

TABLE III.

Comparison of vigour with percentage area of fibres, parenchyma, vessels and rays in the wood.

Wood Growth.		Fibres.		Parenchyma.		Vessels.		Rays.	
Root-stock No.	Metres.	Root-stock No.	%	Root-stock No.	%	Root-stock No.	%	Root-stock No.	%
128	53·9	VII	34·5	VII	24·2	45	21·9	45	22·3
45	53·3	125	34·1	45	28·8	VII	16·5	125	23·6
125	50·6	128	32·0	128	29·0	128	13·1	VII	24·8
VII	43·2	45	27·0	99	30·0	125	11·7	128	26·0
90	36·7	9	25·0	108	30·4	90	10·4	9	34·8
9	32·2	29	23·6	125	30·6	29	8·2	29	36·4
IX	30·5	90	20·2	90	31·2	9	7·7	90	38·2
108	29·7	IX	18·4	29	31·8	IX	6·5	IX	40·4
29	21·5	99	18·3	9	32·4	108	6·4	108	46·7
99	16·0	108	16·5	IX	34·8	99	4·9	99	46·8
Sig. diff. (p. = ·05)	*10·0*		*3·5*		*7·0*		*4·2*		*6·0*

rootstocks are arranged in descending order of vigour for wood growth, percentage area of fibres and vessels, and in ascending order for amount of parenchyma and rays. It is at once evident that there is a marked correlation between the proportion of vessels, fibres, rays, and, to a less extent, parenchyma, and the vigour of the scion. The clearest connection is in the proportion of ray tissue. The same four rootstocks appear at the top of every column except one (amount of parenchyma), though not always in exactly the same order. The same three rootstocks appear in the middle of most columns, and the three others at the bottom. No. 29 has a somewhat greater area of fibres and vessels, and less ray tissue than Nos. 90, 9, 108 and 99, although it has produced very dwarf trees. In two other series of Lane's Prince Albert trees on the same rootstocks, however, the wood growth records show that No. 29 has proved rather more vigorous.

(iii) *Relative Area Occupied by Living and Dead Tissue in the Wood.*

The relative area occupied by living and dead tissue in the wood was calculated by dividing the area of parenchyma plus rays by the area of fibres plus vessels. In the four vigorous rootstocks there was approximately an equal amount of living and dead tissue, whereas in the six more dwarfing rootstocks there was from twice to three times as much living as dead tissue. This can clearly be seen in Table IV and in Figs. 1 to 8.

TABLE IV.

Comparison of vigour with the proportion of living to dead tissue in the wood.

Living : Dead.		Rootstocks in descending order of vigour.
Rootstock No.	Ratio	
VII	1·0	128
45	1·0	45
125	1·2	125
128	1·2	VII
29	2·1	90
9	2·1	9
90	2·4	IX
IX	3·1	108
108	3·4	29
99	3·5	99
Sig. Diff. ($p. = ·05$)	0·94	

(iv) *Relative Number of Fibres, Parenchyma Cells and Vessels in the Wood.*

Counts were made of xylem fibres, xylem parenchyma cells and vessels from the photo-micrographs described above. (See Table V.) The four more vigorous rootstocks had nearly twice as many fibres and, with one exception

TABLE V.

Mean number of xylem fibres and vessels in a microscopic field of unit area.

Rootstock in descending order of vigour.	Xylem fibres.	Vessels.
128	214	7
45	197	14
125	258	10
VII	201	14
90	120	7
9	162	8
IX	113	8
108	103	8
29	131	7
99	108	6

(No. 128), more vessels than the six dwarfing rootstocks. With the above exception, as in the relative areas of the different elements, there was a clear break between the four vigorous and the six more dwarfing rootstocks.

(v) *Relative Size of Fibres, Parenchyma Cells and Vessels in the Wood.*

The area corresponding to unit weight of bromide paper having been first measured, the mean "weights" of a fibre, a parenchyma cell and a vessel were converted into areas, thus giving an estimate of relative cell size.

No definite connection was found between cell size and the vigour of the scion in the fibres and parenchyma cells, but the vessels were generally larger in the more vigorous rootstocks. This is well shown in Figs. 1, 2, 3 and 4. No. VIII was found to have rather large vessels, although it is a dwarfing rootstock (see Fig. 6).

DISCUSSION.

In 1933, Tydeman (5) said that, "In the present state of our knowledge it is quite impossible to make any reliable deduction as to the subsequent influence of a seedling rootstock upon a scion variety from its appearance prior to being worked. An attempt to find morphological characters sufficiently distinctive to make it possible to correlate them with the ultimate performance of the seedling as a rootstock is described elsewhere. . . . The extreme lack of discontinuity in most of the characters studied makes it seem unlikely that this method will ever prove very successful. There is promise that the plant physiologist or biochemist may, in due time, evolve criteria by which the relative capacity of a seedling rootstock to impart vigour or precocity to its scion may be predetermined from the appearance or constitution of the young seedling. In the meantime there is no alternative but to subject the seedlings to the more protracted trials in the field."

The evidence now presented provides at least some indication that the internal structure of the roots may be related to the vigour which an apple rootstock will impart to a scion variety. At present it is not possible to forecast finer differences in vigour and precocity, but new rootstocks may be classified into vigorous and dwarfing groups.

The characters which appear to be most useful as a guide to vigour are: (1) the bark : wood ratio, (2) the percentage of wood ray tissue, (3) the vessel area and (4) the percentage of wood fibres.

If the tendency here shown is retained in older trees, the examination of the internal structure of the roots will enable breeders of new apple rootstocks to classify their seedlings when comparatively young into different groups according to the vigour which they are likely to impart to a scion, and to discard those which are unsuitable in vigour for their purpose.

Knowledge of the correlation between the bark : wood ratio and vigour will be especially valuable in this connection, as the measurements required may easily and rapidly be obtained. It will also be of value in planning nursery trials of new clonal rootstocks, as it will be possible to distinguish between vigorous and dwarfing rootstocks, and this will tend to make the process of testing new rootstocks more rapid and accurate.

Since dwarfing rootstocks have a much higher bark : wood ratio and a higher proportion of wood ray tissue than the vigorous rootstocks, they possess a larger volume of cells capable of storing carbohydrates relative to their size. Trees worked on such rootstocks may, therefore, have relatively greater carbohydrate reserves available for fruit bud formation than those on vigorous rootstocks. At the same time the passage of mineral salts in solution through the small vessels in the wood of the dwarfing rootstocks may be slower than through the large vessels of the vigorous rootstocks, and this may tend to restrict shoot growth. The vigorous rootstocks also possess a much greater mechanical strength (owing to their numerous wood fibres) than the dwarfing rootstocks. It seems likely, therefore, that at least a partial explanation of the mechanism of rootstock effect may be obtained from a study of the internal structure of fruit trees.

SUMMARY.

1. Transverse sections were made of the roots of eighty-six four-year-old apple trees on Nos. VII and IX and on eight new clonal rootstocks, worked with Lane's Prince Albert. The new rootstocks were obtained by crossing the two dwarfing rootstocks Nos. VIII and IX.

A striking correlation was found between the relative area of bark to wood, as seen in transverse section, and the vigour of the scion.

2. Transverse sections of the roots were examined by means of a projection apparatus. Direct negatives were made on bromide paper, showing the structure of the wood of eight new rootstocks and of Malling rootstocks Nos. VII, VIII and IX. The photo-micrographs so obtained were then cut up into the four elements of the wood and weighed in the following groups: (1) fibres, (2) parenchyma, (3) vessels and (4) rays.

(i) The percentage areas of fibres, vessels, rays and, to a less extent, of parenchyma estimated from these photographic prints, was found to bear a marked connection with the vigour of the scion, the clearest connection with vigour being in the proportion of wood ray tissue.

(ii) The four vigorous rootstocks Nos. VII, 45, 125 and 128 were found to have an almost equal amount of living and dead tissue in the wood, whereas the six more dwarfing rootstocks Nos. IX, 90, 9, 108, 29 and 99 showed from twice to three times as much living as dead tissue.

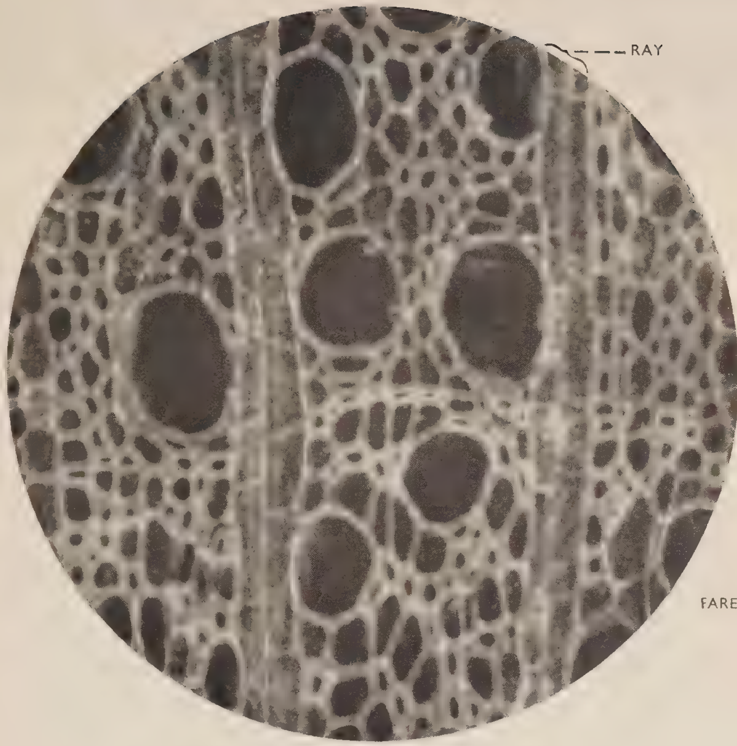


FIG. 1.

T.S. Root, No. 125.

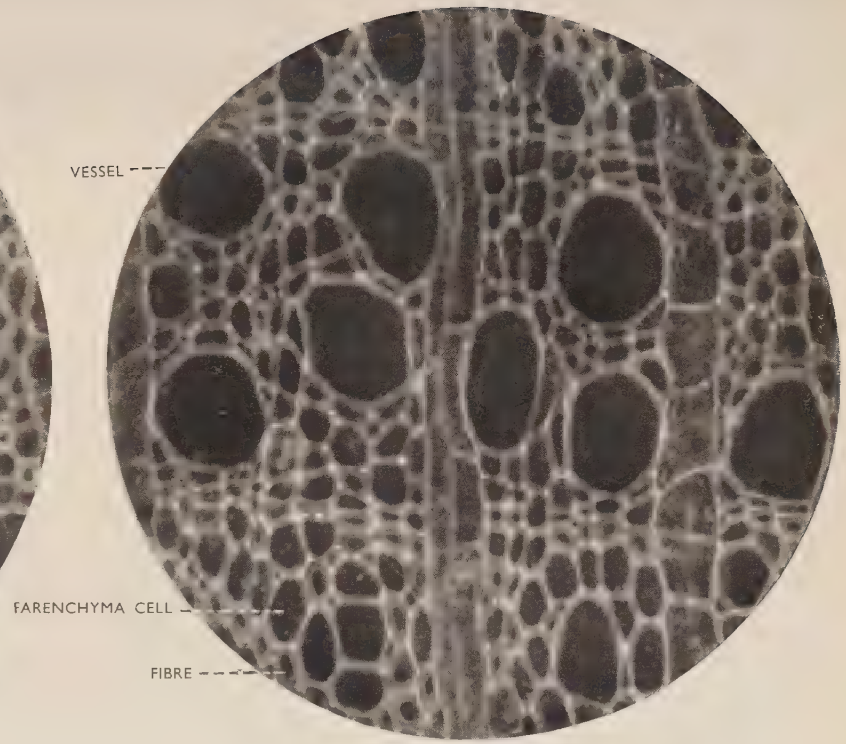


FIG. 2.

T.S. Root, No. 128.

Photo-micrographs of transverse sections of the wood of roots of the new vigorous Apple Rootstocks, Nos. 125 and 128, budded with Lane's Prince Albert (× 290).

Note.—Large vessel area, high proportion of fibres and small amount of ray tissue.

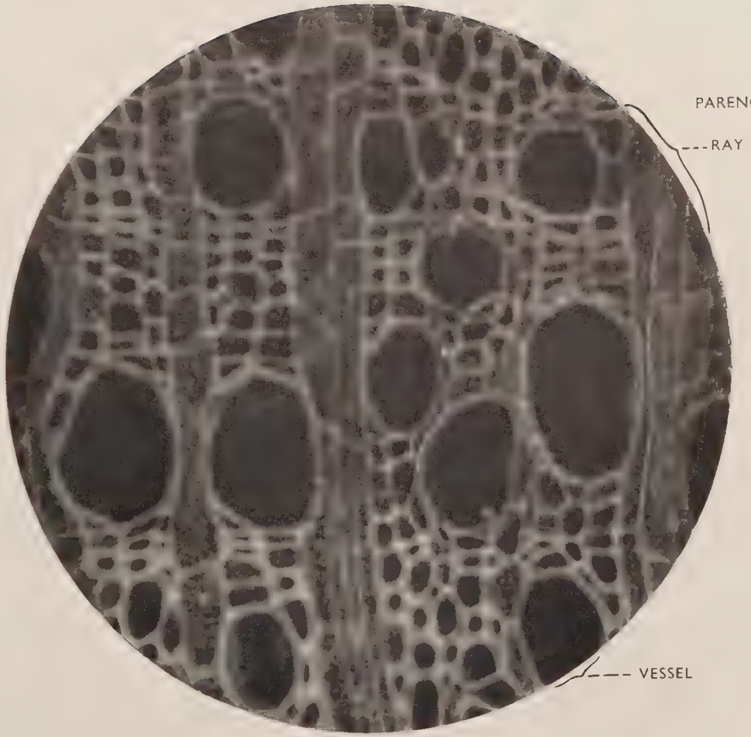


Fig. 3

T.S. Root, No. 45.

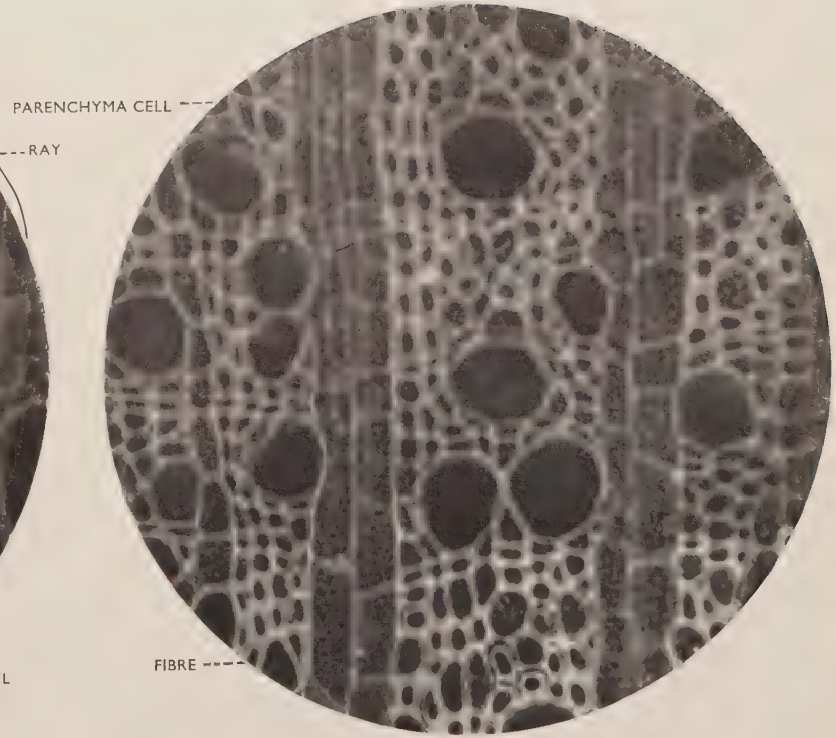


Fig. 4.

T.S. Root, No. VII.

Photo-micrographs of transverse sections of the wood of roots of Rootstocks, Nos. 45 and VII, budded with Lane's Prince Albert × 200.

Note.—Large vessel area, high proportion of fibres and small amount of ray tissue.

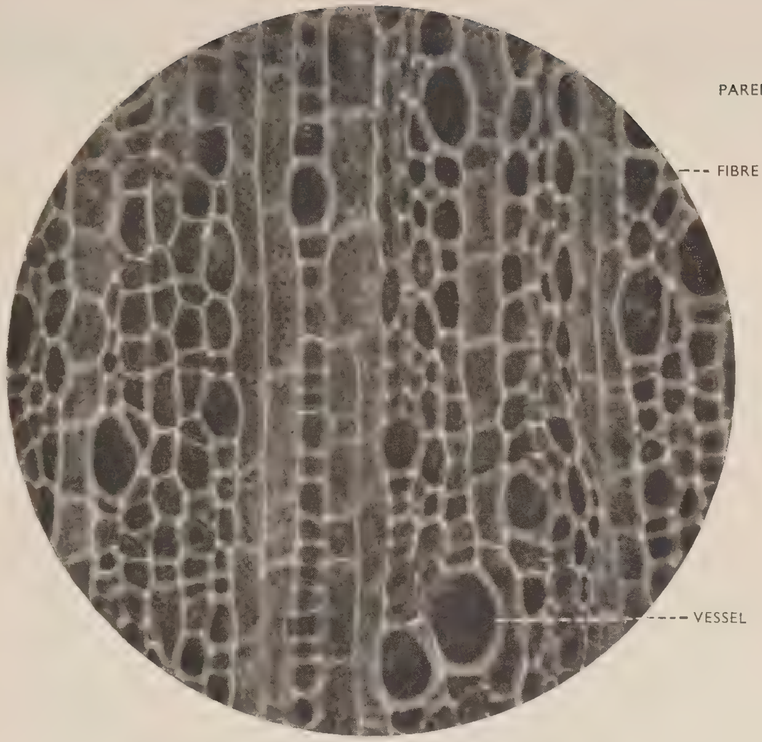


FIG. 5.

T.S. Root, No. 108.

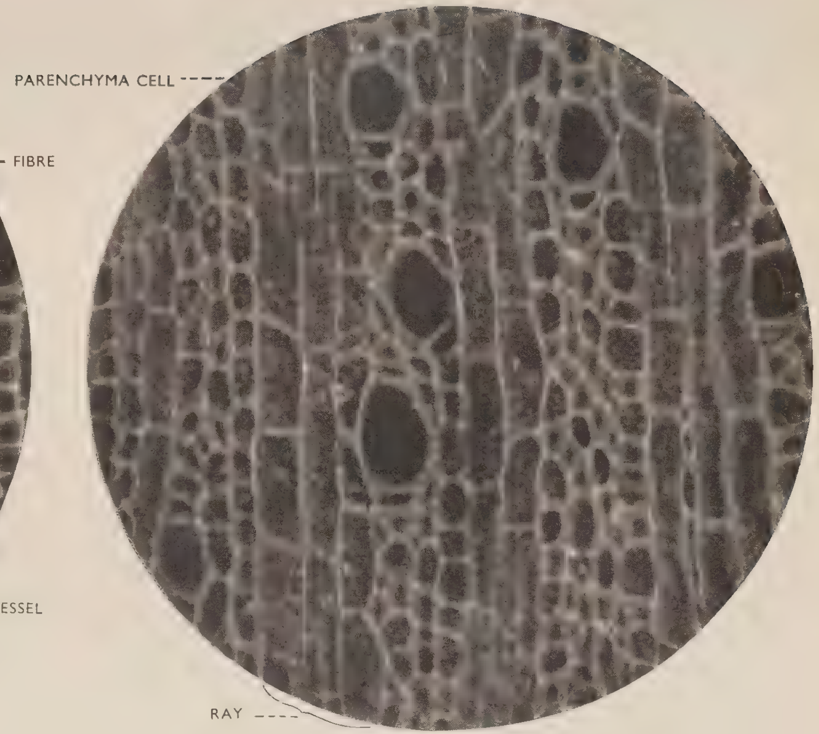


FIG. 6.

T.S. Root, No. VIII.

Photo-micrographs of transverse sections of the wood of roots of Rootstocks Nos. 108 and VIII, budded with Lane's Prince Albert (× 290).

Note.—Small vessel area, low proportion of fibres, and large amount of ray tissue.

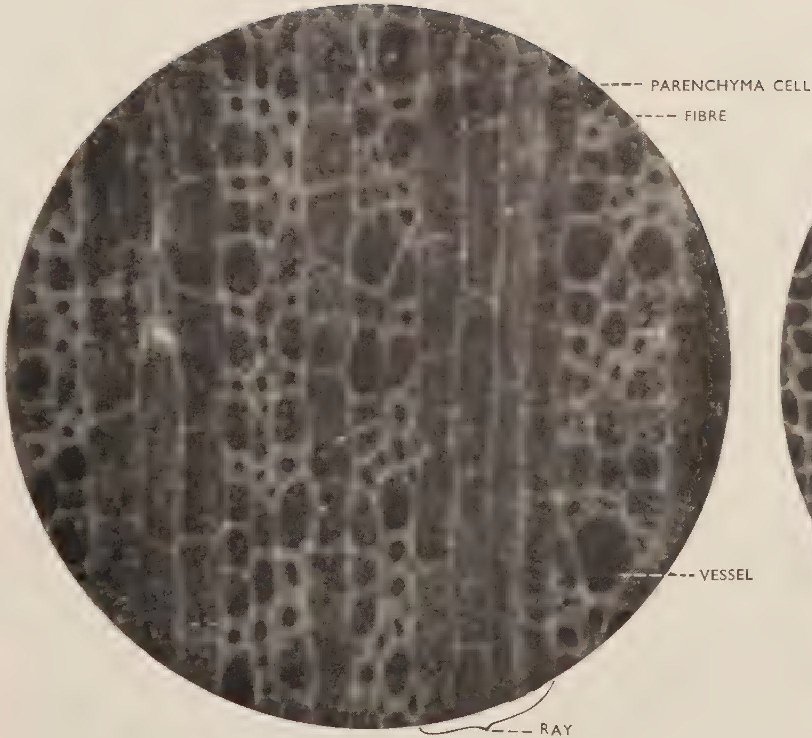


Fig. 7.

T.S. Root, No. IX.

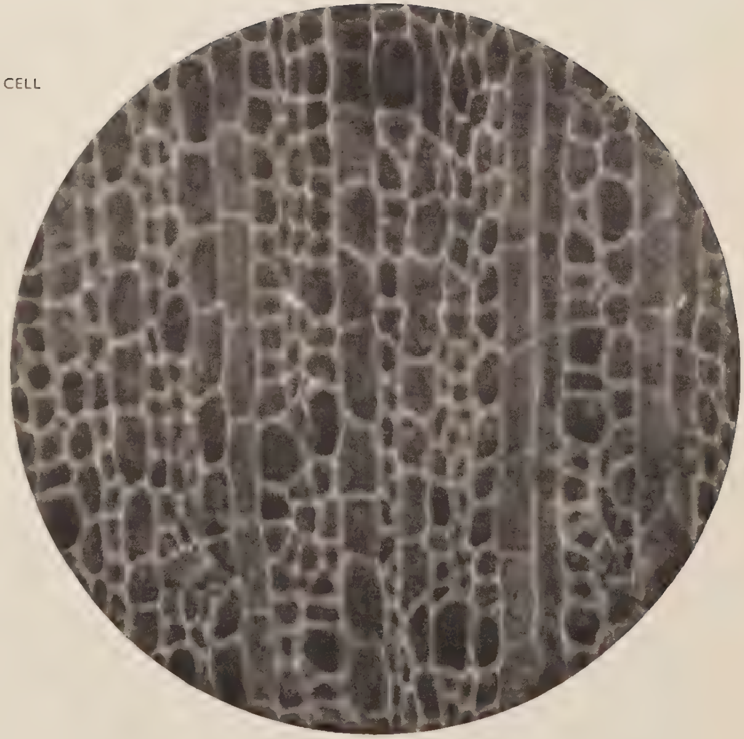


Fig. 8.

T.S. Root, No. 99.

Photo-micrographs of transverse sections of the wood of roots of the dwarfing Rootstocks, No. IX and 99, budded with Lane's Prince Albert (× 290).

Note.—Very small vessel area, low proportion of fibres and very large amount of ray tissue.

(iii) Counts of fibres and vessels in the wood revealed a clear break between the four vigorous and the six dwarfing rootstocks, the former having a larger number of vessels and nearly twice as many xylem fibres as the latter.

(iv) No definite connection was found between the size of the wood elements and the vigour of the scion, but there was a tendency for the more vigorous rootstocks to possess larger vessels than the dwarfing rootstocks.

ACKNOWLEDGMENTS.

The authors wish to express their gratitude to Mr. T. N. Hoblyn for giving valuable criticism and advice in connection with the presentation of this paper and for analysing the data ; and to Mr. H. M. Tydeman for permission to use his wood growth and fruit bud records.

REFERENCES.

(1) *Beakbane, A. B.* and *Renwick, M. E.* A preliminary report on the internal structure of the wood of No. IX rootstock in relation to scion-rooting of apples. East Malling Res. Sta. Ann. Rept. for 1935 (1936), 100.

(2) *Hatton, R. G.* Apple rootstock studies. Effect of layered stocks upon the vigour and cropping of certain scions. Journ. Pom. & Hort. Sci., 1931, **9**, 265.

(3) *Tydeman, H. M.* Studies on new varieties of apple rootstocks. Journ. Pom. & Hort. Sci., 1937, **15**, 165.

(4) ———. The root systems of some new varieties of apple rootstocks. East Malling Res. Sta. Ann. Rept. for 1936 (1937), 87.

(5) ———. The testing of new varieties of apple rootstock. A progress report. East Malling Res. Sta. Ann. Rept. for 1933 (1934), 94.

(6) Glossary of Terms Used in Describing Woods. Reprinted from Trop. Woods, 1933, No. 36, pp. 12.

(*Received* 23/1/39.)

MAGNESIUM-DEFICIENCY OF FRUIT TREES

By T. WALLACE
Long Ashton Research Station, University of Bristol

In sand-culture experiments with various hardy fruit plants at Long Ashton, the symptoms shown in cultures where magnesium has been deficient have always been very striking and the deficiency has resulted in very serious effects on the growth processes of the plants. The main symptoms shown by various magnesium-deficient fruit plants have been described in earlier papers (28, 29, 30) and in the last of these, chemical data were given to show how the deficiency affected the composition of leaves and stems as regards content of dry matter, ash, and the chief ash constituents—calcium, magnesium and potassium. A point which was clearly demonstrated in the experiments was the importance of the Mg/K ratio in the nutrient solution (29).

In view of the character of the effects which result from magnesium-deficiency of fruit plants, the writer has kept a close watch on the possibility of this deficiency being evident in plantations in the main fruit areas of the country, especially in view of the fact that fruit growing in recent years has spread to very poor sandy soils, naturally acid in character and poorly supplied with bases.

A further point of importance in the problem is that it has been necessary to recommend high grade potassic fertilizers, especially sulphate of potash, for general use in fruit plantations owing to the risk of injury which may occur from the use of lower grade potassic materials containing large percentages of chlorides. The high grade potassic fertilizers, however, do not contain magnesium salts, as do the lower grade materials (such as kainit) which are the only commonly used artificial fertilizers that add appreciable amounts of magnesium to the soil.

Where strongly acid, poor, sandy soils are used for fruit growing, the grower begins with a growth-medium very poorly supplied with the three bases, lime, magnesia and potash, required in quantity by fruit plants. The normal procedure to bring such soils into a satisfactory condition for fruit crops would be to apply lime to counteract the acidity and then to supply nitrogen, potash and phosphates by means of fertilizers such as nitro-chalk, calcium cyanamide, sulphate of ammonia, sulphate or muriate of potash, superphosphate, bone manure, etc., none of which contains any appreciable amount of magnesium salts.

It will thus be seen that where magnesium is deficient, nothing is given normally to correct the shortage, and thus magnesium-deficiency may become a problem.

Cases of undoubted magnesium-deficiency in apple trees under such conditions have been observed on certain soils during the past few seasons, and in view of the practical importance of the problem, the evidence obtained is given below and some points of interest in connection with the deficiency are discussed. In particular, it is desired to focus attention on the possible importance of a low magnesium-content of the foliage as a cause of abnormal susceptibility to spray injury. This point is being made the subject of special investigations at Long Ashton.

THE RÔLE OF MAGNESIUM IN PLANTS.

The rôle of magnesium in plant growth has been the subject of numerous investigations during the past 100 years, but even now the part it plays is not clearly understood. As early as 1840, Liebig, on the basis of ash analyses of plants, considered magnesium to be an essential element and, since that time, many laboratory and field experiments have been carried out to show the extent to which vegetative growth and crop yields can be affected by magnesium compounds. The evidence obtained from much of the work has been contradictory, especially in field experiments in which merely increases in yields of crops have been used to measure the effects produced. Many experiments of this type have been carried out in France during recent years by Brioux (4), and they serve to demonstrate only that in many soils the supplies of available magnesium are sufficient for the needs of many agricultural crops.

In other investigations, interest has centred around the Ca/Mg ratio in plant tissues, following on the work reported by Loew (17), who considered that these elements were required in fairly definite proportions in the different parts of plants—the "lime" factor; moreover, that if magnesium content was relatively high the element became toxic. This viewpoint of Loew has been disputed by several workers, e.g. Pfeiffer and Rippel (23), but was supported by results such as those on potatoes at Woburn where lowered yields resulted from the use of magnesium-containing fertilizers (27).

The idea of magnesium toxicity has been further strengthened by the relative infertility of soils derived from rocks of high magnesium content, such as serpentine, although it has been shown that with this material infertility may be caused not by too high a content of soluble magnesium but by a high pH, and by deficiencies of certain ions, mainly nitrate and phosphate (12a); furthermore, that toxic effects may be due to high content of nickel, chromium and perhaps of cobalt (24).

An important contribution towards a knowledge of the function of magnesium in plant growth was made by Willstätter (31), who showed that magnesium is an essential ingredient of the chlorophyll molecule, hence

necessary to the formation of the green colouring matter of plants and therefore of fundamental importance in photosynthesis.

Lack of magnesium has also been stated to be a fundamental cause of the ageing of plants, but this view does not appear to be well founded (19). Magnesium may have other essential functions in plant metabolism apart from its importance in chlorophyll formation, since it has been computed that only a fraction of the amount considered necessary for growth is contained in the chlorophyll itself (less than 0·03% Mg for the chlorophyll portion of dry matter compared with 0·25% total Mg) (11).

As a further rôle magnesium has been associated with phosphorus in metabolic processes, but further evidence of the relationship is required. Magnesium appears to be of importance in seed formation, especially in seeds of high oil content, the magnesium content of which is relatively high (18).

From the literature on magnesium-deficiency one point appears of paramount importance, namely the effect of the deficiency on the quality of the leaf (1, 5, 10, 11, 21, 28, 29, 30). As will be shown below, Mg-deficiency is always characterized by defective foliage, the usual visible symptoms being chlorosis, necrosis of tissue and premature defoliation of the older leaves.

Symptoms and Chemical Features in Magnesium-Deficient Crop Plants.

The symptoms of magnesium-deficiency shown by different plants are very varied in detail, though all show points in common, and it is these points which are valuable in studying cases of suspected Mg-deficiency involving plants for which the particular symptoms are not known. Leaf symptoms are always the most valuable, but the variation in these which may occur even for fruit plants grown in this country will be evident from the previous reports of the present writer (28, 29).

As stated above, the most usual leaf symptoms are chlorosis, necrosis of interveinal tissue and premature fall of the older leaves, which are always the first to show effects. Chlorosis is of common occurrence and usually occurs near the tips and edges of the leaves; later it spreads towards the midrib between the veins, which remain green, as in tobacco. The chlorotic parts subsequently become necrotic, brown and brittle.

In plants in which the leaf veins are parallel, as in maize, chlorotic strips of interveinal tissue alternate with the green veins.

Instead of chlorosis, affected parts may turn palish green in well defined areas and suddenly become brown and dried out, as in apples; or, well defined patterns of colour, generally reds, may develop on the upper surfaces of the leaves, as in black currant, strawberry and cotton.

The portion of the leaf affected may vary even for different varieties of a given class of plants. For example, in apples, the varieties Cox's Orange

Pippin and Allington Pippin tend to show interveinal tissue breakdown in blotches in the centre of the leaf around the midrib, whilst in Bramley's Seedling the majority of the leaves may be affected first around their margins.

Affected leaves are usually very thin and may show characteristic curling or puckering, as in black currant, which shows the former, and spinach, which shows the latter character.

The leaves often form an absciss layer before appearing sufficiently mature to do so, as is well shown in apples ; this, together with the thin character of affected leaves, may be of great significance in problems of spray injury. In severe cases, defoliation is always serious. Leaf fall invariably begins with the oldest leaves and proceeds progressively towards the younger growths.

In the early stages of Mg-deficiency in fruit plants, shoot growth and leaf size are not materially affected ; and, in fact, the loss of lateral leaves may lead to some stimulation of shoot elongation. Eventually, however, shoot growth becomes very dwarfed and leaf size very small (30).

Mg-deficiency is associated with the following chemical features in the leaves: dry matter in the fresh leaf weight is decreased, i.e. the leaf has a relatively high water-content (11, 30); total carbohydrate-content is low, especially starch (8, 11) ; ash in dry matter is high, and magnesium-content of the ash is low (11, 30). In practice, the low magnesium-content may be accompanied by relatively high amounts of calcium and potassium or low ones of calcium (on acid soils) with very high potassium-content (11).

In tobacco, it has been found that where the Mg-content of the leaves falls below 0·25% dry matter (MgO, 0·40%) deficiency symptoms appear (11).

THE OCCURRENCE OF MAGNESIUM-DEFICIENCY IN CROP PLANTS.

Failures due to magnesium-deficiency have been proved in a variety of crop plants, especially in the eastern states of the U.S.A. bordering the Atlantic. Well defined cases have also been reported from Germany, Holland, Belgium and Bohemia in Europe, from New South Wales and from Canada.

In all cases the soils on which the failures occur are of a light sandy texture, usually strongly acid in reaction and poorly supplied with bases ; they occur, also, in situations and under climatic conditions conducive to strong leaching action. A case of Mg-deficiency in oats has recently been recorded in a neutral, sandy soil in a Mitscherlich pot experiment (25).

The outstanding crop to show magnesium-deficiency in the U.S.A. has been tobacco, the condition being known as "Sand Drown", since it is prevalent on sandy soils in wet seasons. Vegetable crops (especially potatoes) and cotton appear to be commonly affected, and cases in maize have also been reported. Buckwheat and spinach are said to be highly susceptible to Mg-deficiency. In Canada, Mg-deficiency has been recorded in potatoes in New Brunswick (20).

In Holland, low magnesium-content of affected plants has been found in cases of the " Hooghalensche " (acidity) disease of cereals (14), and the disease has been completely controlled in oats and other crops by applications of magnesium sulphate (26a). In Bohemia, responses have been obtained to magnesium fertilizers in districts where the magnesium-content of the rocks is low (7). In Belgium, cases of Mg-deficiency in sugar beet are on record (9), and in Germany, in addition to cases in agricultural plants, a case in pine trees (Yellow Tip) has been described (3). In New South Wales, Mg-deficiency has been proved for citrus and vegetable crops (21, 22).

The incidence of magnesium-deficiency has been shown to be related to manurial practices other than the use of magnesium fertilizers. Thus, high potash manuring has been stated to be conducive to Mg-deficiency in various crops, including corn, potatoes and sugar beet (9, 12, 15, 16), and the sulphate ion has been found to increase, and the chlorine ion to decrease, the severity of the trouble in tobacco (10).

In connection with the observations on potash manuring in relation to Mg-deficiency, it is noteworthy that in studies on ion relationships, with maize in nutrient solutions, it was shown that magnesium-content was negatively correlated only with potassium supply (2).

Remedies for Magnesium-Deficiency.

In annual crops magnesium-deficiency has easily been remedied by the addition of moderate dressings of magnesium-containing materials. Epsom salts (hydrated magnesium sulphate), kieserite (anhydrous magnesium sulphate) and sulphate of potash-magnesia have all been found effective and quick acting, at rates supplying from 20 to 30 lb. of soluble magnesia (MgO) per acre, for tobacco and vegetable crops, whilst insoluble compounds such as magnesian limestone and dolomite have proved efficient, at rates between 500-1,000 lb. per acre (5, 6, 11). The latter compounds are naturally slower in action than the soluble compounds but they are especially valuable on acid soils when it is also desired to reduce soil-acidity and to supply calcium.

Crop residues and farmyard manure have also been found of benefit, due presumably to their magnesium-content (10).

Although annual plants deficient in magnesium have been shown to respond quickly to dressings of magnesium-containing fertilizers, it seems probable from results obtained in sand-culture experiments by the writer that fruit trees, such as apples, when severely deficient in magnesium, may recover only very slowly. In one experiment with Bramley's Seedling in sand-culture, deficient trees showed appreciable response to magnesium applications only in the third season of treatment. (Data unpublished.)

EXPERIMENTAL.

The investigations which have been carried out to date have been in connection with apple trees growing at three different centres and so far have consisted in a diagnosis of Mg-deficiency based on leaf symptoms and chemical composition of the leaves. At two of the centres experimental manurial plots for treatment with magnesium sulphate at 4 cwt. per acre, for a period of years if necessary, have been arranged, and at one a trial dressing of magnesian limestone, at 2 tons per acre, has been applied.

At the present stage interest attaches mainly to the conditions of occurrence, manurial history, leaf symptoms and chemical analyses of foliage samples.

CENTRE I.

The site is practically level, with only a very gentle slope to the south, and lies at the foot of a short, steeper, southern slope which falls from a low ridge.

The soil over the greater part of the area is of a light sandy texture in both surface and subsoil, but as the ridge is approached, the subsoil becomes heavier and eventually is of a clayey nature. The problematic areas, so far, are confined to the more sandy sections farthest from the ridge. Drainage in these sections is naturally very free and conducive to excessive leaching, and the soil is naturally strongly acid, carrying a typical acid herbage.

Samples of surface soil were taken from three Blocks in the autumn of 1937 and determinations were made of exchangeable lime, magnesia and potash, using ammonium acetate as the leaching agent. The results were as follows:—

TABLE I.

	Exchangeable CaO %	Exchangeable MgO %	Exchangeable K_2O %
Block A.	0·113	0·004	0·020
Block B.	0·104	0·003	0·019
Block C.	0·144	0·001	0·025

These results indicate a low status for lime and magnesia, with a satisfactory potash value.

The area had been ploughed up from grass in November 1932, and cordon apple trees, mainly Cox's Orange Pippin, James Grieve and Laxton's Superb on Malling No. II rootstock, were planted in January 1933, at 7 ft. × 2 ft. 6 in.

Manuring since planting has varied somewhat in the Blocks over the area but the following for Block C may be taken as typical.

1933. Sulphate of potash, at 5 cwt. per acre, sprinkled around trees at planting. Trees mulched with farmyard manure.

1934. Sulphate of potash broadcast, at 5 cwt. per acre. Poor cover crop of Brown Mustard ploughed in. Epsom salts (magnesium sulphate) broadcast, at 4 cwt. per acre.

1935. Agricultural lime applied, at 1 ton per acre.
Potash salts (30%) ,, ,, 5 cwt. ,, ,,
Sulphate of ammonia ,, ,, 3 ,, ,, ,,
Basic slag, ,, ,, 10 ,, ,, ,,
Poor cover crop of Brown Mustard ploughed in. Epsom salts applied, at 4 cwt. per acre.

1936. Sulphate of potash broadcast, at 5 cwt. per acre (spring).
Agricultural lime ,, ,, 1 ton ,, ,,
Sulphate of potash ,, ,, 5 cwt. ,, ,, (autumn).
Epsom salts ,, ,, 4 ,, ,, ,,

1937. Shoddy (5-6% ammonia) applied, at 2 tons per acre.

TABLE II.

Ash Constituents in Dried Leaves from Centre I. Seasons 1937-38.

Variety—Laxton's Superb.

Season	Area	Ash in Dry Matter	As % Dry Matter.				As % Ash.			
			CaO	MgO	K_2O	P_2O_5	CaO	MgO	K_2O	P_2O_5
1937	Untreated since 1936 ..	6·45	0·86	0·083	2·61	0·179	13·33	1·29	40·46	2·78
	Manured area including Mg Sulphate 1934, 35, 36	6·44	0·79	0·081	2·54	0·170	12·27	1·26	39·44	2·10
1938	Untreated ..	5·70	0·80	0·15	2·22	—	14·1	2·6	39·0	—

A small area in this Block has not been given the magnesium sulphate dressings and has been left unmanured since 1936.

In the above manurial programme the following points should be noted: potash manuring has been very heavy; lime and phosphates have both been given; three heavy dressings of Epsom salts have been applied in an endeavour to correct magnesium-deficiency.

The trees at this centre have made rather strong growth and, being cordons, have been subjected to severe pruning. Three main troubles have been experienced: spray damage has been very serious and it has been impossible to carry out a normal spray programme; each season leaf fall from current season's shoots, especially in the terminals, has been serious; the trees have dropped their fruit each year in the June-July period.

The trees have been inspected by the writer on three occasions—September 15th, 1936, August 23rd, 1937 and August 15th, 1938. In the two former years the trees had been summer pruned prior to the visits, which rather complicated the leaf symptoms, nevertheless there was considerable evidence of magnesium-deficiency, shown as blotching of the older leaves and defoliation of shoots. In 1938 the shoots had not been summer pruned, and on this occasion the symptoms were less in evidence, even on the unmanured area.

Foliage samples were taken for analysis in 1937 and 1938, the leaves being taken from near the bases of terminal shoots and, as far as possible, showing the typical magnesium-deficiency breakdown symptoms. The results appear in Table II.

Centre II.

The site consists partly of a very gentle slope to the north and partly of a flat area at the top of the slope. The soil has not been examined in detail over the whole field, but for the greater part it consists of a very light, coarse sand to a considerable depth, and is derived from Greensand material. The soil conditions are generally similar to those of the sandy area at Centre I, and before amelioration they were typically those of a sandy podsol.

Data obtained on samples of surface soil and subsoil, taken in January 1939, are given in Table III.

Table III.

Mechanical Fractions.	Surface Soil %	Subsoil %
Coarse Sand	68·50	73·50
Fine Sand	18·31	20·60
Silt	4·15	3·00
Clay	3·75	2·60
Moisture	0·93	0·57
Loss on Solution	0·42	0·57
Loss on Ignition	1·29	0·69
$CaCO_3$	Nil.	Nil.
pH	6·60	6·90
Exchangeable CaO	0·380	0·174
,, MgO	$<$0·001	$<$0·001
,, K_2O	0·016	0·005

The mechanical analyses reflect the coarse sandy nature of the soil. The chemical results show that although no free calcium carbonate remains in the soil from previous dressings yet the pH is fairly high and the reaction only slightly acid. Exchangeable CaO in the surface soil is appreciably higher than at Centre I, but exchangeable MgO is even less, and the values in both surface

soil and subsoil are extremely low. Exchangeable potash is at a moderate level in the surface soil and low in the subsoil sample.

Bush apple trees, varieties Cox's Orange Pippin, Laxton's Superb and Miller's Seedling, on Malling No. I rootstocks for permanent trees and on No. IX for fillers (Miller's Seedling on No. II for these), were planted during the winters 1935-36 and 1936-37, the permanent trees being at 20 ft. square with the fillers interplanted at 10 ft.

Cropping and manuring since 1933 have been as follows:—

1933. Mustard and roots and fed off with sheep.
Superphosphate 3 cwt., kainit 2 cwt., per acre.

1934. Barley.
Sulphate of ammonia 1 cwt., superphosphate 2 cwt., kainit 2 cwt., per acre.

1935. Oats.
Compound corn fertilizer, 5 cwt. per acre.

Winter 1935-36. Section planted with apples.
Carbonate of lime 1 ton, sulphate of potash 3 cwt., per acre.

Winter 1936-37. Remainder of field planted with apples.
Sulphate of potash, 3 cwt. per acre.

Winter 1937-38. Sulphate of potash, 4 cwt. per acre.

Spring 1938. Nitro-chalk, 1 cwt. per acre.

TABLE IV.

Ash Constituents in Dried Leaves from Centre II. Season 1938.

Variety—Cox's Orange Pippin. Rootstock M.I.

Ash in Dry Matter.	As % Dry Matter.				As % Ash.			
	CaO	MgO	K_2O	P_2O_5	CaO	MgO	K_2O	P_2O_5
9·0* ..	1·34	0·09	3·76	0·73	14·9	1·0	41·8	6·4

* High value for ash in dry matter probably denotes severe nature of magnesium-deficiency at this centre.

In the winter of 1937-38, four rows through the plantation were treated with nitro-chalk at 3 cwt. per acre, and two rows with Epsom salts at 4 cwt. per acre, to ascertain the effects of these materials on premature defoliation. These special treatments did not produce any clear effects in 1938.

Growth has been variable throughout the plantation and there have been areas of poor growth, especially on the flat portion, where the trees have shown considerable defoliation and stunting of shoot growth. When examined in August 1937 and 1938, magnesium-deficiency symptoms were strongly in

evidence where defoliation was taking place, and in 1938, especially in certain areas, many trees were practically defoliated, and even the top rosettes often showed severe breakdown symptoms.

Leaf samples from a poor area on the flat portion were taken for analysis in August 1938 from trees of Cox's Orange Pippin on No. I rootstock. The results are given in Table IV.

CENTRE III.

This centre comprises Plot 14 at the East Malling Research Station. The site is practically level and forms part of an old river terrace. The parent material of the soil is mainly derived from the Lower Greensand (Hythe Beds) formation, which the superficial terrace deposit overlies. The texture of both surface and subsoil is generally a fine sandy, light to medium loam, with occasional somewhat more sandy patches in the subsoil layers.

Samples of surface soil and subsoil were obtained for analysis in January 1939, the samples being representative of areas which have received two different levels of potash manuring during recent years (see below).

The results appear in Table V.

TABLE V.

Mechanical Fractions.	Rows 14 and 16 Double Potash Manuring.		Rows 10 and 12 Single Potash Manuring.	
	Surface Soil %	Subsoil %	Surface Soil %	Subsoil %
Coarse Sand	21·67	22·01	22·96	20·10
Fine Sand	47·79	46·49	51·20	47·60
Silt	12·72	14·10	11·28	14·62
Clay	10·62	12·50	10·65	12·75
Moisture	2·36	2·23	2·06	1·81
Loss on Solution	3·03	2·03	1·35	1·21
Loss on Ignition	1·23	1·15	3·17	2·35
$CaCO_3$	Nil.	Nil.	Trace.	Trace.
pH	7·6	7·7	7·2	7·8
Exchangeable CaO	0·291	0·280	0·438	0·360
,, MgO	0·0130	0·012	0·009	0·008
,, K_2O	0·071	0·031	0·063	0·018

The data show a general similarity for the two areas, although there are points of difference.

The textures in the two cases are similar, both being fine sandy, light loams. The amount of free calcium carbonate is either nil or very low, although pH values are inclined to be above neutral point. Exchangeable CaO differs somewhat in the two areas and the values are not very different from that of the surface soil at Centre II. The values for exchangeable MgO are higher than at

the other two centres, although they are still low. Exchangeable potash in the surface soils is very high as also is that for the subsoil of the Double Potash area. The values reflect the difference in potash treatments of the areas and also the liberal potash dressings which have been applied in recent years.

The area has been used as an experimental apple plantation since 1920 when the varieties Bramley's Seedling and Worcester Pearmain on several kinds of rootstock were planted. From 1920 to 1931 the area was left unmanured, during which time potash-deficiency effects became prevalent over the plot. From 1931 onwards the plot has been divided into sub-plots for the differential treatments—no manure, potash only, nitrogen only, and nitrogen plus potash. Nitrogen has been applied annually as sulphate of ammonia at 4 cwt. per acre, and potash as sulphate of potash at 4 cwt. per acre in 1931 and at 8 cwt. per acre from 1932 onwards. The latter rate for potash, which is abnormally high, was given purposely to study the effects of very heavy dressings on the speed of recovery from potash-deficiency. From 1935 the potash treatment was given to all plots. In the winter of 1934-35, the Worcester trees were removed as the plantation had become overcrowded.

In July 1936, following the manurial treatments stated above, practically all the Bramley trees on the plot were making healthy growth and carrying heavy crops of fruit, and the previous potash-deficiency appeared to have been overcome. Later in the season, however, other symptoms were noted on the leaves of several trees, being particularly marked on those on No. III rootstock. These took the form of browning between the veins and marginal scorching with upward curling of the edges of the leaves. The symptoms appeared most intense on trees receiving the " no nitrogen " treatment. There was some doubt as to the interpretation of the symptoms, and leaf samples were taken for analysis from trees on No. III rootstock undergoing the various manurial treatments.

The results are presented in Table VI.

TABLE VI.

Ash Constituents in Dried Leaves from Centre III. Season 1936.

Variety—Bramley's Seedling on Rootstock M.III.

Manurial Treatment 1931-1934.	Ash in Dry Matter %	As % Dry Matter.				As % Ash.			
		CaO	MgO	K_2O	P_2O_5	CaO	MgO	K_2O	P_2O_5
N+K*	6·73	2·03	0·10	1·75	0·47	30·16	1·54	26·0	7·01
K	6·59	1·85	0·07	1·86	0·48	28·11	1·13	28·3	7·34
N	7·31	2·37	0·12	1·60	0·43	32·44	1·64	22·0	5·91
Nil.	7·76	2·62	0·11	1·60	0·42	33·76	1·39	20·6	5·40

* All plots received sulphate of potash at 8 cwt. per acre in seasons 1935 and 1936.

DISCUSSION.

The soil conditions at Centres I and II are typical of those on which magnesium-deficiency has usually been found, viz.: light, sandy soils, freely drained, originally acid in reaction and showing typical characters of podsolized soils. At Centre III the natural conditions would be considered less favourable to the development of Mg-deficiency and there the manurial history may be an important factor. The leaf symptoms at Centres I and II were generally of the centre "blotching" type which is easily recognized, but at Centre III, where the variety is Bramley's Seedling, the symptoms were not so clear. It would appear also that the trouble is much more serious at Centres I and II, especially at the latter. In both cases defoliation has been considerable and, at Centre II, shoot growth has been seriously affected. The values for exchangeable MgO in the soils are in the order III>I>II, which agrees with the field observations of Mg-deficiency effects.

TABLE VII.

Seasonal Cycles of Ash and Ash Constituents in Dried Leaves of Apple Trees, variety Lane's Prince Albert on Malling No. II rootstock, grown under favourable conditions at Long Ashton. Season 1934.

Month of Sampling.	Ash in Dry Matter %	As % Dry Matter.				As % Ash.			
		CaO	MgO	K_2O	P_2O_5	CaO	MgO	K_2O	P_2O_5
June	6·39	1·54	0·44	1·68	0·65	24·14	6·92	26·30	10·25
July	6·73	1·52	0·42	1·92	0·52	22·64	6·26	28·60	7·73
August	6·97	1·73	0·42	1·82	0·41	24·86	6·04	26·18	5·86
September ..	7·50	2·02	0·45	1·92	0·40	26·93	6·04	25·67	5·27
October	7·82	2·28	0·45	1·67	0·33	29·16	5·77	21·37	4·26
November	6·74	2·40	0·49	1·13	0·22	35·66	7·21	16·83	3·29

In order to show the significance of the chemical data for the foliage, Table VII has been prepared, which shows the normal amounts of ash and ash constituents in the leaves of apple trees over a growing season, when supplies of nutrient elements are present in amounts suitable for balanced growth. The leaves are from Lane's Prince Albert apple trees on Malling No. II rootstock growing at Long Ashton and given suitable manurial treatment. The composition of these leaves compares well with that of leaves from trees at other English centres where conditions appear to allow of good, healthy growth.

Points requiring attention in Table VII are as follows: The seasonal trends in the ash and in the various ash constituents, in which the amount of magnesia remains a fairly definite proportion of both dry matter and ash throughout the season; the amounts of lime, magnesia and potash in the dry matter, the

amounts of the two former agreeing well with the amounts stated by Garner *et al.* (11) as necessary for the healthy growth of the tobacco leaf, viz. above 1·0% CaO and 0·4% MgO ;* the amounts of the three bases in the ash, especially MgO, which approximates to 6·0% (cf. the results of Davis, Hill and Johnson (8) for strawberries with a complete nutrient solution, viz. 5·0% to 6·0% MgO). When the results for the three centres are compared with those in Table VII it will readily be seen that in all of them the magnesia content both in dry matter and in ash is very low and, indeed, is typical of the amounts reported in cases of severe magnesium-deficiency for other crops.

A point of difference between Centre III and the other two Centres is the low amount of lime at each of the two latter. These results point to the fact that at Centres I and II lime is also relatively deficient, as would be expected under acid soil conditions,† whereas at Centre III magnesia is the only deficient constituent.

At Centres I and II potash dominates the ash, obviously because it is the only base which has hitherto been available to the trees in quantity, and under such circumstances there may be considerable luxury consumption of this base which may tend to aggravate the low magnesia supply (2, 12).

The results reported in Table II suggest that the three heavy dressings of magnesium sulphate given prior to 1937 had not appreciably affected the magnesium-content of the leaves in that year. This may mean that recovery from the deficiency may be slow, as indicated in the pot experiments of the writer.

The question arises as to what measures should be taken to avoid magnesium-deficiency in fruit trees in soils such as occur at Centres I and II. These soils, being originally acid, are naturally deficient in the three bases, lime, magnesia and potash. Normally, lime and potash would be adequately supplied by the usual fertilizer programmes, in which lime and various forms of calcium phosphate supply lime, and sulphate of potash provides potash. Magnesium, however, is not usually given, excepting where farmyard manure and plant residues are applied, and hence is liable to be deficient.

The cheapest form of magnesia for acid soils is undoubtedly magnesian limestone which, in addition to providing magnesium, also supplies calcium and reduces soil acidity. It has been found an effective source of magnesium for annual plants in various countries at rates of 500 to 1,000 lb. per acre, and there is no reason to expect that it would not be efficient, although perhaps rather slow in action, for fruit trees. Quick-acting magnesium salts, such as Epsom salts, kieserite and sulphate of potash-magnesia, would also be suitable, and

* Parbery also found an average of 0·41 per cent. MgO on the leaves of healthy citrus trees and an average of 0·096 MgO in chlorotic (magnesium-deficient) leaves.

† In view of the values for pH and Exchangeable CaO for the soil samples at Centre II, calcium-deficiency would not normally be expected, but it may be that the CaO from the 1935-36 lime application has not yet become sufficiently available to the roots of the trees.

occasional dressings of such materials at a rate of approximately 1 cwt. per acre would perhaps be sufficient to prevent the onset of the deficiency in the majority of cases. It must be remembered, however, that these quick-acting magnesium fertilizers do not contain calcium, and thus unless this element is supplied in some form on strongly acid, leached soils, the provision of adequate supplies of magnesia and potash may lead to a relative deficiency of calcium. This has been known to occur in tobacco on soils similar as regards natural base status to those at Centres I and II (11).

Where magnesium-deficiency occurs on neutral soils or on soils containing free carbonate of lime, in which the calcium status is satisfactory or high, the quick-acting magnesium salts would always be preferable. Centre III is a case where the calcium status is apparently satisfactory. At this centre it seems most probable that the high potash manuring practised in recent years, following the period of no manurial treatment, has caused a relative deficiency of magnesium. The higher potash dressings, NK and K series, as compared with N and Nil series, are shown in Table VI to be associated with lower amounts of lime and magnesia in dry matter and ash.

Liberal potash manuring has been shown in many cases in practice to be conducive to magnesium-deficiency but, as has been pointed out by Beckenbach *et al.* (2), the depressing action of one ion on the absorption of another, such as potassium on magnesium, is not so important as the actual concentrations of the ions in the nutrient medium. Thus, in such cases as at Centre III, although a reduction in potash level might be of appreciable benefit, the most satisfactory method of remedying Mg-deficiency would be to apply a magnesium fertilizer.

CONCLUSIONS AND SUMMARY.

1. An account is given of previous work relative to magnesium-deficiency in crop plants. It is shown that the deficiency is of common occurrence in annual plants in certain parts of the U.S.A. and Europe, generally on light, sandy soils of acid reaction and subject to excessive leaching by rain, and has also been reported in citrus and vegetable crops in New South Wales.

2. The possible rôle of magnesium in plants is discussed, and reference is made to the relationship of magnesium to calcium and potassium, and to the problem of magnesium toxicity in plants.

3. The possible importance of magnesium-deficiency in problems of spray injury is indicated.

4. Evidence of magnesium-deficiency in apple trees at three centres in England is given, and it is shown how the composition of the leaves of terminal shoots may be used to determine the condition of the foliage with regard to supplies of lime, magnesia and potash.

5. Where supplies of calcium and magnesium are adequate in apple leaves, the amounts present are similar to those in tobacco leaves of satisfactory quality.

6. Methods of treating soils with magnesium-containing materials in cases of magnesium-deficiency are given.

ACKNOWLEDGMENTS.

Thanks are due to Dr. F. F. Kay, Reading University, for carrying out the soil determinations in Table I and the leaf analyses given under 1937 in Table II.

Mr. W. A. Bane and Dr. W. A. Roach have been associated with the writer in the investigations at Centre III.

The data in Table VII are taken from an investigation by Dr. V. G. Vaidya carried out under the direction of the author.

REFERENCES.

(1) *Beaumont, A. B.* and *Snell, M. E.* The Effect of Magnesium Deficiency on Crop Plants. Journ. Agr. Res., 1935, **50**, 553.

(2) *Beckenbach, J. R., Robbins, W. R.* and *Shrive, J. W.* Nutritional Studies with Corn. II. A Statistical Interpretation of the Relation between the Ionic Concentration of the Culture Solutions and the Element Content of the Tissues. Soil Sc., 1938, **45**, 403.

(3) *Becker-Dillingen, J.* The "Yellow Tip" Disease of Pine Trees, a Symptom of Magnesium Deficiency. Die Ernähn. der Pflanze., 1937, **33**, 1 and 19.

(4) *Brioux, C.* The Fertilizing Effect of Magnesium. Ann. Agron., 1935, **5** (N.S.), 190.

(5) *Carolus, R. L.* Effects of Magnesium Deficiency in the Soil on the Yield, Appearance and Composition of Vegetable Crops. Proc. Amer. Soc. Hort. Sc., 1934, **31**, 610.

(6) *Chucka, J. A.* Magnesium Studies with the Potato. Proc. Amer. Soc. Hort. Sc., 1937, **35**, 534.

(7) *Cosse, V.* Magnesia and Lime in some Bohemian Soils. Imp. Bur. Soil Sc., Soils and Fertilizers, List 35, p. 6.

(8) *Davis, M. B., Hill, H.* and *Johnson, F. B.* Nutritional Studies with Fragaria. II. Scient. Agric., 1934, **14**, 411.

(9) *Decoux, L.* and *Rowland, G.* Imp. Bur. Soil Sc., Soils and Fertilizers, List 72, p. 22.

(10) *Garner, W. W., McMurtrey, J. E.* and *Bacon, C. W.* Sand Drown, a Chlorosis of Tobacco due to Magnesium Deficiency and the Relation of Sulphates and Chlorides of Potassium to the Disease. Journ. Agr. Res., 1923, **23**, 27.

(11) *Garner, W. W., McMurtrey, J. E., Jr., Bowling, J. B.* and *Moss, E. G.* Magnesium and Calcium Requirements of the Tobacco Crop. Journ. Agr. Res., 1930, **40**, 145.

(12) *Gehring, A., Creutzburg, et al.* Further Studies on the Effect of Magnesium on the Productivity of Soils. Ztschr. Pflanz. Düng., 1933, 29A, 335.

(12a) *Gordon, A.* and *Lipman, C. B.* Why are Serpentine and other Magnesian Soils Infertile. Soil Sc., 1926, **22**, 291.

(13) *Anon.* Imp. Bur. Soil Sc., Monthly Letter No. 66, April 1937.

(14) *Itallie, T. B. van.* The "Hooghalensche" Disease and the Composition of Cereals. Imp. Bur. Soil Sc., Soils and Fertilizers, List 57, p. 20.

(15) *Jones, J. P.* Deficiency of Magnesium the Cause of a Chlorosis in Corn. Journ. Agr. Res., 1929, **39**, 873.

(16) *Knoblauch, H. C.* and *Odland, T. E.* A Magnesium Deficiency induced by previous Fertilizer Treatments. Journ. Amer. Soc. Agron., 1934, **26**, 609.

(17) *Loew, O.* The Liming of Soils from a Physiological Standpoint. U.S.D.A., Bur. Plant Indust. Bull. 1, 1901.

(18) ———. The Physiological Rôle of Mineral Nutrients. U.S.D.A., Div. Veg. Physiol. and Path. Bull. 18, 1899.

(19) *Lutman, B. F.* and *Walbridge, N. L.* The Rôle of Magnesium in the Ageing of Plants. Vermont Agric. Expt. Stn. Bull. 296, 1929.

(20) *Macleod, D. J.* and *Howatt, J. L.* Magnesium Deficiency in Potatoes. Imp. Bur. Soil Sc., Soils and Fertilizers, List 47, p. 23.

(21) *Parbery, N. H.* Mineral Constituents in Relation to Chlorosis of Orange Leaves. Soil Sc., 1935, **39**, 35.

(22) ———. Magnesium Deficiency in Cabbages and Cauliflowers. Imp. Bur. Soil Sc., Soils and Fertilizers, 1938, **1**, 40.

(23) *Pfeiffer, F.* and *Rippel, A.* Der Einfluss von Kalk und Magnesia auf das Wachstum der Pflanzen. Journ. Landw., 1920, **68**, 5.

(24) *Robinson, W. O.* and *Byers, H. G.* Chemical Studies of Infertile Soils derived from Rocks high in Magnesium and generally high in Chromium and Nickel. U.S.D.A. Tech. Bull. 471, 1935.

(25) *Scharrer, K.* and *Schropp, W.* A Typical Case of Magnesium Deficiency on Neutral Sand Soil. Die Ernäh. der Pflanze., 1938, **34**, 366 and 388.

(26) *Schmitt, L.* New and Old Ideas about Magnesia Fertilizing. Imp. Bur. Soil Sc., Soils and Fertilizers, List 57, p. 13.

(26a) *Stieltjes, D.* Some Observations on the Hooghalen and Reclamation Diseases on the Mineral Experimental Field at De Eeese near Steenwijk. (Translated Title.) Landbouwk. Tijdschr., 1937, **49**, 844.

(27) *Voelcker, J. A.* The Woburn Field Experiments. Journ. Roy. Agric. Soc., England, 1900, **70**, 362.

(28) *Wallace, T.* Experiments on the Manuring of Fruit Trees. I. Journ. Pom. & Hort. Sci., 1925, **4**, 117.

(29) ———. Experiments on the Manuring of Fruit Trees. II. *Ibid.*, 1925, **5**, 1.

(30) ———. Experiments on the Manuring of Fruit Trees. III. *Ibid.*, 1930, **7**, 23.

(31) *Willstätter, T.* and *Stoll, A.* Untersuchungen über Chlorophyll. Berlin, 1913.

(*Received* 24/1/39.)

EFFECTS OF VARIATION IN THE SUPPLY OF POTASH TO LETTUCES GROWN UNDER GLASS

By R. M. WOODMAN
Horticultural Research Station, Cambridge University

THE present paper describes two experiments carried out to discover the effects of deficiencies in the supply of potassium on the growth, yield, and appearance of lettuces grown as sand cultures under glass. The work is a logical continuation of similar experiments described elsewhere on the same crop with phosphorus and nitrogen as the variants (1, 2, 3).

EXPERIMENTAL.

In the first experiment, the glazed culture-jars which were used each held about 46 lb. of a fine, white, pure, silica sand that has been previously described (1).

The first six nutrient solutions (A-F) were identical except for a variation in the potassium sulphate content. The concentrations of important elements present are given in Table I. The AnalaR salts used in making the solutions were: sodium nitrate, as the source of nitrogen ; anhydrous disodium phosphate, as the source of phosphorus ; potassium sulphate, as the source of potassium (and sulphur) ; a solution of calcium chloride, made by neutralization of calcium carbonate with hydrochloric acid, as the source of calcium ; magnesium sulphate heptahydrate, as the source of magnesium (and sulphur) ; and ferrous sulphate heptahydrate, as the source of iron (and sulphur). The minor elements were

TABLE I.

Parts per Million of Certain Elements in the Solutions.

Solutions.	N.	P.	K.	Ca.	Mg.	Fe.	S.	Na.
For 1st Experiment :								
A.	16·48	43·70	89·76	36·12	20·20	0·50	63·73	91·88
B.	16·48	43·70	67·32	36·12	20·20	0·50	54·53	91·88
C.	16·48	43·70	44·88	36·12	20·20	0·50	45·33	91·88
D.	16·48	43·70	22·44	36·12	20·20	0·50	36·13	91·88
E.	16·48	43·70	11·22	36·12	20·20	0·50	31·53	91·88
F.	16·48	43·70	Nil.	36·12	20·20	0·50	26·93	91·88
G.	Nil.	Nil.	44·88	Nil.	Nil.	0·50	18·69	Nil.
For 2nd Experiment :								
AI.	16·48	5·46	44·88	18·06	5·05	0·50	25·35	35·18
BI.	16·48	5·46	22·44	18·06	5·05	0·50	16·15	35·18
CI.	16·48	5·46	16·83	18·06	5·05	0·50	13·85	35·18
DI.	16·48	5·46	11·22	18·06	5·05	0·50	11·55	35·18
EI.	16·48	5·46	5·61	18·06	5·05	0·50	9·25	35·18
FI.	16·48	5·46	0·56	18·06	5·05	0·50	7·18	35·18
GI.	16·48	5·46	Nil.	18·06	5·05	0·50	6·95	35·18

found to be unnecessary in these cultures. The seventh solution (G) contained potassium and ferrous sulphates only, other salts being absent.

In the first experiment there were twelve replications of each of the first five treatments A-E, and these sixty cultures were arranged in an unheated greenhouse as a "layout" of twelve randomized blocks. There were only three cultures for each of the treatments F (no potash) and G (potash and iron alone), and these six cultures therefore were not contained in the randomized-block arrangement.

Sowing of the lettuce, variety May King, was made on May 25th, 1936, in the sand in the culture-jars, so that the seed actually germinated in contact with the particular nutrient solution concerned, and there was thus no transplanting to check growth and develop the coloration of this tinted lettuce (2). The seedlings were later thinned out to give the arrangement of five seedlings necessary for five harvests (2). The temperature of the greenhouse was high, even though unheated, and ranged between the extreme limits 50-104° F., but usually at first from 50-80° F. and, in the last three weeks of the experiment, from 60-80° F. The period as a whole could not be considered very bright for that time of the year. Thus, the daily averages of the hours of sunshine were: 1st week, commencing on May 30th, when some seed had germinated, 5·5; 2nd week, 5·0; 3rd week, 8·0; 4th week, 8·2; 5th week, 4·5; and the 6th week, ending on the day of the harvest of mature lettuce, July 10th, 4·3.

Because the seedling harvests with solution E yielded seedlings of approximately the same weight and size as with treatments A, B, C and D, which all contained more potash, the amount of potash present in this solution was successively reduced on three occasions, June 17th, June 26th and July 1st. These reductions were to 5·61, 2·81 and 1·12 p.p.m. of potassium in the solution, respectively; the resulting concentrations of sulphur then present in this solution E were 29·23, 28·08 and 27·39 p.p.m.

The second experiment was commenced on June 30th, 1937, in ordinary plant-pots (16 (large) to the cast, each pot, 9 in. in diameter, holding about 13 lb. of the sand), as glazed culture-jars were not available at the time. The pots were coated on the outside with three coats of copal varnish, and were then immersed in boiling paraffin "refined" (m.p. = 110° F.) for 30 min. In the randomized-block arrangement used, 7 treatments were replicated 16 times, making 112 cultures in all.

The concentrations of certain elements in the solutions used are given in the second half of Table I: the "potash-alone" treatment was omitted, but the "no-potash" treatment was expanded to a full treatment (GI); the range of concentrations of potassium used was only the lower half of that in the first experiment, and low concentrations were thus explored more fully, especially with the extra potash treatment, FI.

During the course of the second experiment, $8\frac{1}{2}$ litres of solution were applied to the cultures, usually in 250-c.c. lots three times a week. As, towards maturity, the low phosphate content of the solutions tended to give lettuces with purple flushes (1, 2), the sodium phosphate content was quadrupled on August 16th, 1937, so that they now all contained 21·85 p.p.m. of phosphorus ; the cultures then rapidly became green (2).

OBSERVATIONS ON THE CULTURES.

First Experiment: May 25th, 1936: Day of Sowing. June 3rd, 1936: Germination complete. June 3rd, 1936: The seedlings were thinned to 5 per pot (2). June 4th, 1936: The cultures dripped freely on addition of fresh solution. June 15th, 19th, 22nd and 26th, 1936: The dates of the four seedling harvests. July 10th, 1936: The harvest of the mature lettuces from the central seedlings.

Second Experiment: June 30th, 1937: Day of sowing. July 6th, 1937: Germination complete. July 8th, 1937: The cultures were singled to a central seedling. July 14th, 1937: The cultures dripped freely on addition of fresh solution. August 31st, 1937: Harvest.

Notes made during the experiments are summarized below:—

APPEARANCE AND TINTING OF CULTURES.

1st Expt.: The seedlings at germination were all green ; in two days with G (potash alone), the seedlings were darker green, and tinged with red at the edge. As the experiment progressed, these plants were the darkest green of all the cultures, and still later became dull-bronze. The plants were stunted, with flat, smooth leaves ; they had a typical flat, rosette appearance, reminiscent of the same lettuce with phosphate alone (2).

There was developed, during growth, a slight deepening in the shade in passing from A-F, though the green of the F cultures (no potash) was never so dark as that encountered with G. Ultimately the cultures with F turned chlorotic green.

At the age of about three weeks, the cultures with F (no potash) had a very characteristic appearance. The leaves were smaller than for normal plants, and had wider veins. The leaves also were not so flat ; this was not due to a wavy leaf as a whole, but to the fact that the portions between the veins all tended to be convex on the upper surface, so that a "crinkly" and typically "starved" appearance resulted. These convex portions were darker green than was normal ; but later, as previously stated, the plants became rather chlorotic in appearance. There was also finally a tendency for the leaf margins to curl upwards towards the upper surfaces of the leaves. As a result of scorch (see later), cultures with F presented a typically tall, narrow appearance.

2nd Expt. : There was not much difference in tint. The treatments with least potash gave plants of a more erect habit of growth as a result of scorch.

SCORCH :

1st Expt. : This appeared with cultures with E and F after about four weeks. Brown dead patches (showing up the network of the leaf structure) and marginal scorch appeared on the outer (oldest) leaves ; this was followed by limpness, and finally by absolute withering, of the whole leaf. The scorch due to this deficiency or absence of potash always worked inwards from the oldest leaves towards the heart. All the E cultures were severely affected, but the absolute disappearance of the outer leaves with some of the cultures left lettuces which could be placed in Grade I at harvest. The cultures with F (no potash) were so consistently and badly affected, and the outer leaves withered so rapidly, that all growth seemed to be upwards, so that a characteristically high, narrow, erect plant finally resulted.

2nd Expt. : Somewhat similar effects were obtained, and earlier here, especially with treatments EI, FI and GI. There was similar marginal scorch extending inwards, and patches of scorched tissue broke away and left holes in the leaves. As the older leaves withered and died off, the plants were, at times, not so bad in appearance. The treatment without potash (GI) did not lead to such immature, small, erect plants as in the first experiment, possibly because, as perceived from the size and weight, these plants must have obtained some potash from somewhere. As "spot" tests failed to show the presence of potash in the sand, this potash might have come from the plant-pots, which, at the end of the experiment, were found to be wetted by water despite the boiling in wax which they had undergone ; or the sodium present in the solution might have replaced the missing potassium to some extent (4).

Scorch of this lettuce due to lack of potash was also confirmed by water-culture experiments made in 1938.

SIZE :

Linear measurements of the cultures were made weekly: the greatest spread, and the breadth of the culture at right angles to this.

In the first experiment there was at no time much difference with treatments A-E, though C always tended to give slightly the smallest cultures and E slightly the largest, and, but for the severe scorch and withering away of the outer leaves of cultures with E, these might have been larger still finally. Treatments F and G gave small cultures. At harvest the means of these measurements in cm. were: A, 22·3 × 20·9 ; B, 22·2 × 21·4 ; C, 21·4 × 19·8 ; D, 21·9 × 20·7 ; E, 22·6 × 21·3 ; F, 8·3 × 5·7 ; and G, 3·0 × 2·0.

In the second experiment, for the first three weeks, the treatments with least potash gave smaller cultures. As the experiment progressed, the sizes

became more uniform, until at harvest they were, in cm.: AI, $26{\cdot}1 \times 24{\cdot}1$; BI, $25{\cdot}7 \times 23{\cdot}3$; CI, $25{\cdot}7 \times 23{\cdot}7$; DI, $25{\cdot}0 \times 22{\cdot}8$; EI, $25{\cdot}4 \times 23{\cdot}3$; FI, $25{\cdot}0 \times 22{\cdot}5$; and GI, $25{\cdot}1 \times 22{\cdot}7$. The results with GI demonstrated that these cultures were obtaining potash, possibly from the pots, as previously explained. The results in general confirmed those for the first experiment in one important point, that potash over a wide range had apparently little effect on size, very small amounts of available potash yielding good-sized plants (cf. ref. (4)).

HEARTING:

The numbers of lettuces which were fully hearted and hearting up (the latter values are in parentheses) with the various treatments in the first experiment at harvest were: A, 9 (3); B, 6 (6); C, 7 (5); D, 7 (5); E, 8 (4); F, 0 (0); G, 0 (0). Thus, increasing the dose of potash beyond that in E (which gave deficiency symptoms for potash as regards scorch, if not as regards size and weight) did not cause earlier maturity (cf. the earlier maturity for this crop with increased supplies of phosphate (2) and nitrogen (3)).

Corresponding figures for the second experiment at harvest were: AI, 4 (8); BI, 5 (10); CI, 4 (10); DI, 4 (12); EI, 3 (13); FI, 0 (16); and GI, 1 (13); in addition, 4 of AI, and 1 each of BI and CI, had flower-stems forming, which stopped hearting. The conclusion drawn as regards maturity from the first experiment was therefore confirmed.

ROOTS:

With A, B, C, D and E, in the first experiment, the roots were normal, well-developed, and bushy tap-roots; F gave a small, undeveloped root, lacking in fibre; G gave the smallest roots, with long, coarse, hair-like laterals. Similar results were obtained in the second experiment, except that F and G were about half the size of the roots with treatments A-E.

GRADE:

The numbers of lettuces judged to be first grade at harvest in the first experiment were: A, 9; B, 6; C, 7; D, 7; E, 3; F, 0; G, 0. With A, B, C and D, the remaining lettuces at harvest were spoilt by the appearance of flower-stems or by immaturity; with E, scorch also was responsible to a large extent. Results which bore these out were obtained for the second experiment.

THE YIELD WITH DIFFERENT TREATMENTS.

The values obtained for each culture were the fresh weights in g. of the top (cut off at the junction of top with stalk), root, and total plant; the corresponding dry weights, the top/root ratio for fresh and dry weights, and the percentage moisture contents of the fresh material of the top, root, and total plant.

The actual data of the experiment were too bulky to be reproduced, but are available for examination in this laboratory. The analyses of variance (5) were worked out for the fresh and dry weights of the tops, roots, and total plants; the top/root ratios for fresh and dry weights, and the percentages of moisture in the tops, roots, and total plants. The corresponding summaries of results for the two experiments are tabulated in Tables II and III, together with the standard errors of the treatment means (5). Arithmetical (and not weighted) means have been used when dealing with ratios and percentages (2).

KEY TO THE TABLES OF SUMMARIES OF RESULTS.

The first column is "Description of Data". "FW" and "DW" denote fresh and dry weights; the figures I, II, III, IV and V, the 1st, 2nd, 3rd and 4th seedling-harvests, and the main harvest, for the 1st experiment.

In the next column there occurs, for each Summary of Results, one of the descriptions S, SS, SSS or NS, which indicates that the treatment means were significant in the (unpublished) tables of analyses of variance, according to Fisher's Tables of z, at the 5%, 1% and 0·1% levels, or were not significant, respectively.

The treatment means are recorded under the "Treatment Mean for" column subheadings. The mean of all the results for a sub-table (which is also the mean of the treatment means) is given in the next column; the standard errors of the treatment means are recorded in the column labelled "S.E."

In the second line of the sub-tables containing the results which had been proved to be significant as above, is given a summary of the comparisons of significance carried out on the treatment means. The signs "$=$" and "$>$" are to be read as "not significantly different from" and "significantly greater than", respectively (2).

The "no-potash" (F) and "potash-alone" (G) results for the first experiment are averages of three cultures for each treatment, and are tabulated in the two columns after the "S.E." one; only the results for treatments A-E were included in the randomized-block system, and the mean and S.E. apply in this experiment, therefore only to these five treatments, and not to F and G.

DISCUSSION OF RESULTS.

The fresh weights of the plants: In the first experiment the results were not significant (NS) during the greater portion of the life of the plant, especially with the maturer lettuce; the weights for the roots at maturity were an exception, however, and were highly significant (SS), though even here $A = B = C$, and the potassium had to be reduced to 22·44 p.p.m. before an increased root system resulted.

TABLE II.

Summaries of Results.

Description of Data.				Treatment Mean for: A.	B.	C.	D.	E.	Mean of all Results.	S.E.	F.	G.
First Experiment.												
Tops	FW.	NS.	I.	0·377	0·385	0·346	0·421	0·407	0·3870	0·02198	0·054	0·021
		S.	II.	0·936	1·057	0·831	0·928	0·796	0·9097	0·06092	0·056	0·022
				B>C=E ; A=B=D ; A=C=D=E.								
		NS.	III.	2.622	2·675	2·826	2·698	2·528	2·686	0·1551	0·140	0·028
		NS.	IV.	5·597	5·469	4·797	5·292	5·792	5·389	0·3389	0·312	0·047
		NS.	V.	32·37	34·41	25·93	32·31	29·84	30·97	2·073	4·964	0·112
Roots	FW.	SSS.	I.	0·034	0·053	0·054	0·048	0·049	0·0476	0·003371	0·021	0·023
				B=C=D=E>A.								
		NS.	II.	0·069	0·092	0·078	0·085	0·078	0·08033	0·005822	0·027	0·015
		SSS.	III.	0·224	0·240	0·286	0·229	0·152	0·2265	0·01231	0·010	0·018
				C>A=B=D>E.								
		NS.	IV.	0·646	0·609	0·618	0·725	0·736	0·6669	0·03917	0·026	0·030
		SS.	V.	8·466	10·03	10·26	12·45	11·09	10·46	0·7018	0·257	0·075
				D>A=B=C ; D=E>A ; B=C=E.								
Total Plants	FW.	NS.	I.	0·411	0·438	0·400	0·469	0·456	0·4346	0·02395	0·075	0·044
		S.	II.	1·005	1·149	0·909	1·013	0·874	0·9900	0·06390	0·083	0·037
				B>C=E ; A=C=D=E ; A=B=D.								
		NS.	III.	2·846	2·915	3·112	2·927	2·680	2·896	0·1565	0·150	0·046
		NS.	IV.	6·243	5·572	5·415	6·017	6·528	6·048	0·3653	0·338	0·077
		NS.	V.	40·84	44·44	36·19	44·76	40·92	41·43	2·466	5·221	0·186

Description of Data.				Treatment Mean for: A.	B.	C.	D.	E.	Mean of all Results.	S.E.	F.	G.
Tops	DW.	S.	I.	0·028	0·029	0·026	0·030	0·033	0·0290	0·001520	0·004	0·003
				E>A=C; A=B=C=D; B=D=E.								
		SS.	II.	0·088	0·104	0·092	0·113	0·110	0·1013	0·004905	0·007	0·003
				B=D=E>A; D=E>A=C; B=C.								
		NS.	III.	0·197	0·209	0·219	0·229	0·230	0·2168	0·01042	0·048	0·009
		NS.	IV.	0·435	0·447	0·441	0·480	0·509	0·4623	0·02496	0·190	0·007
		NS.	V.	2·568	2·772	2·325	2·900	2·713	2·656	0·1326	0·375	0·026
Roots	DW.	SSS.	I.	0·006	0·008	0·007	0·006	0·005	0·006467	0·0003482	0·002	0·003
				B>A=D=E; B=C>E; A=C=D.								
		SSS.	II.	0·021	0·024	0·027	0·036	0·024	0·02642	0·0006108	0·006	0·004
				D>C>B=E>A.								
		SSS.	III.	0·048	0·051	0·058	0·060	0·061	0·05562	0·001048	0·006	0·007
				C=D=E>B=A.								
		SS.	IV.	0·072	0·076	0·079	0·097	0·084	0·08175	0·004107	0·004	0·007
				D>A=B=C=E.								
		NS.	V.	1·289	1·276	1·323	1·596	1·409	1·379	0·1042	0·024	0·021
Total Plants	DW.	NS.	I.	0·034	0·037	0·033	0·036	0·038	0·03547	0·001697	0·006	0·006
		SSS.	II.	0·109	0·128	0·119	0·149	0·134	0·1277	0·005150	0·013	0·007
				D=E>A; D>B>A; D>C; A=C; B=C=E.								
		S.	III.	0·245	0·260	0·277	0·289	0·291	0·2724	0·01089	0·054	0·016
				D=E>A; A=B=C; B=C=D=E.								
		NS.	IV.	0·507	0·480	0·521	0·577	0·593	0·5433	0·02810	0·197	0·014
		NS.	V.	3·857	4·048	3·648	4·497	4·123	4·034	0·2244	0·399	0·047

Description of Data.				Treatment Mean for: A.	B.	C.	D.	E.	Mean of all Results.	S.E.	F.	G.
Top/Root	FW.	SSS.	I.	11·54	7·48	6·63	9·14	8·59	8·675	0·5381	2·62	0·92
				A>D>B=C; D=E>C; B=E.								
		SS.	II.	14·13	11·88	10·86	11·15	10·45	11·69	0·6665	2·31	1·50
				A>B=C=D=E.								
		SSS.	III.	11·80	11·09	10·01	12·33	17·21	12·49	0·6292	15·02	1·55
				E>A=B=C; E>D>C; A=B=C.								
		S.	IV.	8·70	8·21	7·84	7·46	7·86	8·151	0·3329	11·75	1·63
				A>D; A=B=C=E; B=C=D=E.								
		SSS.	V.	3·864	3·415	2·654	2·635	2·698	3·053	0·1998	19·08	1·484
				A=B>C=D=E.								
Top/Root	DW.	SSS.	I.	4·43	3·64	3·99	5·38	6·11	4·708	0·2462	2·17	1·00
				D=E>A>B; D=E>C; A=C; B=C.								
		SSS.	II.	4·28	4·35	3·35	3·15	4·60	3·945	0·1877	1·28	0·83
				A=B=E>C=D.								
		NS.	III.	4·11	4·09	3·75	3·81	3·79	3·908	0·1827	8·50	1·31
		S.	IV.	6·16	5·40	5·90	5·00	6·06	5·743	0·2574	5·33	0·96
				A=C=E>D; A=B=C=E; B=D.								
		NS.	V.	2·014	2·180	1·784	1·941	1·928	1·970	0·1179	14·80	1·265
Tops; % Moisture ..		SS.	I.	92·51	92·58	92·43	92·85	91·91	92·45	0·1575	91·97	84·21
				A=B=C=D>E.								
		SSS.	II.	90·56	90·01	88·90	87·73	85·70	88·58	0·3677	87·51	86·57
				A=B>C>D>E.								
		SSS.	III.	92·39	92·07	92·19	91·44	90·82	91·78	0·1478	60·77	66·35
				A=B=C>D>E.								
		SSS.	IV.	91·28	91·70	90·79	90·86	91·15	91·32	0·0635	37·85	85·58
				B>A=E>C=D.								
		SSS.	V.	92·01	91·85	91·11	90·94	90·86	91·36	0·2102	92·27	76·19
				A=B>C=D=E.								

Description of Data.			Treatment Mean for: A.	B.	C.	D.	E.	Mean of all Results.	S.E.	F.	G.
Roots; % Moisture	SSS.	I.	80·46	84·12	87·18	87·58	88·66	85·60	0·7633	90·32	85·52
			C=D=E>B>A.								
	SSS.	II.	67·85	72·57	63·66	56·05	66·14	65·42	2·425	76·91	74·71
			A=B=E>D; B>C>D; A=C=E.								
	SSS.	III.	78·05	78·11	79·17	72·04	57·23	72·94	1·813	44·55	59·22
			A=B=C>D>E.								
	SSS.	IV.	88·78	87·41	87·19	86·26	88·51	87·63	0·3514	86·05	79·76
			A=E>B>D; A=E>C; B=C; C=D.								
	SS.	V.	84·81	87·27	86·85	87·29	87·24	86·69	0·4932	89·76	72·14
			B=C=D=E>A.								
Total Plants; % Moisture	SS.	I.	91·54	91·60	91·77	92·34	91·57	91·76	0·1609	91·51	84·91
			D>A=B=C=E.								
	SSS.	II.	89·09	88·62	86·74	85·13	84·08	86·73	0·2459	84·28	81·74
			A=B>C>D>E.								
	SSS.	III.	91·31	90·89	91·06	90·01	89·00	90·45	0·1612	60·13	63·44
			A=B=C>D>E.								
	SSS.	IV.	91·76	91·26	90·38	90·32	90·85	90·91	0·1903	41·74	82·24
			A=B>C=D; A>E; B=E; C=D=E.								
	S.	V.	90·52	90·82	90·00	89·88	89·88	90·22	0·2471	92·13	74·55
			B>C=D=E; A=B; A=C=D=E.								

TABLE III.

Summaries of Results.

Description of Data.			Treatment Mean for: AI.	BI.	CI.	DI.	EI.	FI.	GI.	Mean of all Results.	S.E.
Second Experiment.											
Tops	FW.	SSS.	45·34	44·98	42·96	39·06	38·58	32·23	33·49	39·52	0·9333
			AI=BI=CI>DI=EI>FI=GI.								
Roots	FW.	SSS.	16·82	16·81	14·75	11·87	12·48	6·449	7·514	12·39	0·8191
			AI=BI=CI>DI>FI=GI ; AI=BI>EI>FI=GI ; CI=EI ; DI=EI.								
Total Plants	FW.	SSS.	62·16	61·79	57·71	50·93	51·07	38·67	41·00	51·90	1·618
			AI=BI=CI>DI=EI>FI=GI.								
Tops	DW.	SSS.	2·313	2·294	2·285	2·036	2·028	1·479	1·628	2·009	0·0870
			AI=BI=CI>FI=GI ; AI>DI=EI>FI=GI ; BI=CI=DI ; BI>EI ; CI=DI=EI.								
Roots	DW.	SSS.	1·336	1·151	1·151	0·904	0·976	0·488	0·472	0·9254	0·0921
			AI=BI=CI=EI>FI=GI ; AI>DI>FI=GI ; BI=CI=DI=EI.								
Total Plants	DW.	SSS.	3·649	3·445	3·436	2·941	3·004	1·968	2·100	2·934	0·1505
			AI=BI=CI>DI>FI=GI ; AI>EI ; BI=CI=EI>FI=GI.								
Top/Root	FW.	SSS.	2·85	2·74	2·98	3·46	3·32	6·61	5·26	3·889	0·4142
			FI>GI>AI=BI=CI=DI=EI.								
Top/Root	DW.	SSS.	2·03	2·05	2·13	2·44	2·47	4·27	4·26	2·808	0·3162
			FI=GI>AI=BI=CI=DI=EI.								
Tops ; % Moisture ..		S.	94·89	94·90	94·69	94·79	94·75	95·39	95·15	94·94	0·1659
			FI>AI=BI=CI=DI=EI ; FI=GI ; AI=BI=CI=DI=EI=GI.								
Roots ; % Moisture		NS.	92·20	93·13	92·29	92·47	92·48	92·66	93·79	92·72	0·3655
Total Plants , % Moisture		SSS.	94·15	94·43	94·07	94·25	94·17	94·96	94·91	94·42	0·1749
			FI>AI=BI=CI=DI=EI ; FI=GI ; BI=GI ; GI>AI=CI=DI=EI.								

It was evident, therefore, that the fresh weights of the plants were unaffected over a wide range of concentrations of potassium, the main response being with the roots, where more potassium than the optimum, 22·44 p.p.m., decreased growth (cf. ref. (4)). That some potassium was necessary for good growth of both tops and roots was clearly shown by the results with F (no potash) ; here absence of potash resulted in small tops, roots and total plants.

In these experiments all the potash applied was available to the cultures ; and, as it is generally understood that comparatively large quantities of potash should be applied in outside practice to get good growth of this crop, apart altogether from their use from other considerations, such as resistance to frost and scorch, it can be assumed that these amounts are necessary only because potash is not usually readily available after admixture with the soil.

The corresponding results for the second experiment were highly significant ; but, even here, AI = BI = CI for tops, roots and total plants, which demonstrated a lack of response to potash over a wide range, 44·88-16·83 p.p.m. The decrease commenced with DI (11·22 p.p.m., equivalent as regards potash content to E of the first experiment) ; and the root system also with EI (5·61 p.p.m.) was quite good and statistically equal to those for CI and DI. Though FI = GI were both significantly less than all the other treatments for tops, roots and total plants, they were still substantially large, and demonstrated that such small amounts of potash as could be derived from the pots and/or sand, even after immersion of the pots in boiling paraffin, were all that were necessary for moderately good growth. (Response to potash, and small plants in its absence, have been obtained with the lettuce Cheshunt Early Giant in similar pots with a different bulk sample of the same type of sand (unpublished data) ; but the main reason for the second experiment here was to prove conclusively that a response to potash was not obtained over a wide range, and it was thus thought that traces of potash obtained from the pots or sand would not seriously affect this question, as has in fact actually been shown by the experiment ; cf. ref (4) in this connexion.)

It is worthy of note that, in both experiments, a deficiency of potash demonstrated itself by serious scorch before the deficiency was so great as to lead to a serious diminution in growth (6).

The dry weights of the plants : Somewhat similar results were obtained as for the fresh weights, and there was again a marked lack of response to potash over wide ranges of concentration (4). Thus, for the tops, roots and total plants, in the second experiment, AI = BI = CI, while, in the first, the results were not significant. In the second experiment, FI = GI were both significantly smaller than with all other treatments in the three comparisons, but still they were substantially large. The results with F (no potash) in the first experiment,

however, demonstrated that entire lack of potash resulted in stunted growth and correspondingly small dry weights for tops, roots and total plants.

Top/root ratios: For the fresh weights at maturity the differences were highly significant, and demonstrated that, in general, the fresh weights of the tops were favoured more by increased potash than those of the roots, whose weights were actually increased by reduction in potash to the optimum amount of 22·44 p.p.m.; the corresponding ratios for the dry weights were not significant. In the second experiment the results were highly significant for both the fresh and dry weights, and showed that though over a wide range, AI-EI, the ratios were statistically equal (thus going a long way to bear out the results of the first experiment), the very small quantities of potash provided by the treatments FI and GI in the second experiment (0·56 and 0 p.p.m., respectively, plus any traces from pots and/or sand, but both much less than E, 11·22-1·12 p.p.m., in the first experiment) favoured the tops rather than the roots.

The moisture contents of the plants: The results were all highly significant for the first fourteen comparisons in the first experiment, and significant in the fifteenth (per cent. moisture in the total plant at maturity, V). In general, with the tops, decrease in potash supply below B resulted in a decrease in the moisture content; with the roots, at the mature stage, the provision of more potash seemed to give no response over a wide range (B-E), but ultimately (treatment A, V) led to a decrease. The second experiment, in the cases of the tops and total plants (the results with the roots were not significant), also tended to prove the lack of response in this respect over large ranges of concentration; here a very low concentration of potassium, FI = 0·56 p.p.m., was found to give the highest moisture content, and GI also gave, both for the tops and total plants, results statistically equal to FI.

ACKNOWLEDGMENTS.

I thank Messrs. T. W. McKean and J. F. Leonard for their great help during these experiments.

SUMMARY.

Experiments with the object of ascertaining the effects of variation in the potassium content of the nutrient solution on the growth, yield and appearance of lettuces grown in sand cultures under glass are described.

Over a wide range of concentration there was very little response of May King lettuce grown in sand to potassium. Quite small amounts, such as might at times be derived from unglazed pots and/or sand, could also give moderately good growth, though an entire absence of potash resulted in a small plant. It is possible that the ready availability of the potassium supplied in culture

experiments to the plants is responsible for the small amount then required, in contradistinction to the comparatively large amounts recommended in actual practice when growing in soil.

Lack of potash at first gave a leaf of slightly darker green, but later tended to chlorosis. Scorch also resulted with small amounts, and serious scorch was obtained with amounts of potash which did not cause a serious reduction in size ; so that sometimes mature and normal-sized lettuces were obtained which still suffered badly from lack of potash, as shown by the serious scorch. Absence of potash resulted in such rapid, severe scorch and withering away of the older leaves, that ultimately a characteristically small, narrow, relatively tall and erect plant resulted ; the parts of the leaves of these plants between the abnormally-wide veins were convex on the upper surface, and gave the leaves a characteristic, wavy appearance ; these parts were at first darker green than normal, but later became chlorotic.

Large applications of potash did not appear to induce earlier maturity of this lettuce, as large applications of nitrogen or phosphate do.

REFERENCES.

(1) *Woodman, R. M.* Pure Silica Sand as a Basis for Phosphate Deficiency Tests on Lettuce. Sands, Clays and Minerals, 1936, **3**, 22.

(2) ———. Studies in the Nutrition of Vegetables. Phosphate Deficiency and Yield Tests on Sand Cultures of May King Lettuce. Journ. Agric. Sci., 1939, **29**, 229.

(3) ———. Studies in the Nutrition of Vegetables. The Effects of Variation in the Nitrogen Supply on Sand Cultures of May King Lettuce. Ann. Botany, 1939, N.S.**3** (in print).

(4) *Miller, E. C.* Plant Physiology. McGraw-Hill Book Co., 1931, pp. 254, 282, 283.

(5) *Wishart, J.* and *Sanders, H. G.* Principles and Practice of Field Experimentation. The Empire Cotton Growing Corporation, 1935, pp. 15 *et seq.*

(6) *Eckstein, O.*, *Bruno, A.* and *Turrentine, J. W.* Potash Deficiency Symptoms. Verlagsgesellschaft für Ackerbau m.b.H., Berlin, SW11, 1937, p. 5.

(*Received* 28/1/39.)

BOOK REVIEWS

THE GENETICS OF GARDEN PLANTS. By M. B. CRANE and W. J. C. LAWRENCE. Second Edition. (Macmillan & Co. Ltd., London, 1939, pp. 264, Bibliography and Index. 12s. 6d. net.)

The first edition of this by now well-known work was reviewed on page 78 of Volume XIII of this Journal. This, the second edition, follows the same lines as the first as is to be expected, for no revolutionary advances in the subject have occurred in the four years intervening between the two editions. The appearance of a second edition in so short a time is evidence not only of the interest of horticulturists in genetics, but also of the success of the book. In the new edition the final chapter on the origin of new and improved forms has been rewritten and enlarged and a new chapter on the chemical and genetical basis of flower colour has been incorporated. Other sections have been revised and new results added, and there are new sections such as those on linkage in maize and on the genetics and cytology of Iris species. An appendix giving a list of chromosome numbers of some cultivated plants makes its appearance in this edition.

In view of the importance of the book, the only one of its kind in the English language, some criticism is justified. The account of the theory of genetics and cytology, though fundamentally sound, is, on the one hand, rather too concise for the beginner and, on the other, not sufficiently accurate for the advanced student. The reader who has no knowledge of genetics would be well advised to read a good elementary textbook, such as Ford's " The Study of Heredity " or Grüneberg's " Elementary Genetics ".

A chapter on the history of horticultural plant breeding would not only have been of great interest in itself but would have brought out more clearly the relation of genetics to practice and would have afforded an opportunity of assessing the work of such famous breeders as Burbank and Michurin, who held genetics in very low esteem. Historical references of considerable interest are plentiful in the book, but by scattering them throughout the text, as they have done, the authors fail to extract their full historic value.

If the book is examined in detail numerous points on which there is room for more than one opinion emerge. For instance, in the new section on xenia, the authors suggest that the term " metaxenia " is redundant, that " xenia " could profitably be used for the influence of pollen on purely maternal tissue, and that no special term is needed for the effect of pollen on zygotic tissue, since this latter effect is quite easily explained genetically. If these recommendations could be brought into general effect they would possibly be better than the present usage ; but since the two terms xenia and metaxenia are at present in use for two different but related phenomena, and since the few people who use them seem quite clear about their application, there seems little point in suggesting a new usage. The wisest recommendation would probably be to avoid using such recondite terms at all.

It might also be mentioned that a vast amount of work on the genetics of garden plants finds no reference in the book, but this criticism is less valid since

a textbook of this order of size must obviously be very selective, and the authors seem to have done their selection well.

On the credit side it can be said that the book gives a great amount of detailed information of a high standard of reliability. A careful study of this book will give a good grounding in the subject, and it is moreover a useful work to have at hand for reference to the cytology and genetics of particular plants. In spite of the criticisms raised above, the authors are to be congratulated on having produced a textbook of more than average standard. The production of the book is excellent and the slightly increased price is apparently due solely to the increase in size of some fifty pages. J.L.F.

SCIENTIFIC HORTICULTURE. Vol. VII, 1939, pp. 212. (The Horticultural Education Association. 4s. net.)

The appearance of this annual publication is always an interesting event. It provides a cross-section of the present position in horticultural research and education which is of the greatest value, especially to those who have not the time or the opportunity to see original reports and publications. The policy of publishing authoritative summaries of specialized lines of research and regional surveys of horticultural progress is one to be commended.

The practice of publishing the papers read at the Annual Conference of the Association in the previous autumn has been begun in this volume, and will presumably be continued in future. In the present case nearly half of the volume is occupied by the extremely useful short papers presented by the members of the staff of the East Malling Research Station at the Conference in September 1938. Dr. Hatton gives an admirably concise account of the root-stock work at the Station and this is followed by two papers by Grubb on the influence of an intermediate stem-piece and on winter pruning experiments. The new methods of frameworking fruit trees, developed originally in New Zealand and Australia and now causing so much interest in this country, are described in a practical article by Garner and Walker. Space does not permit of detailed mention of all the papers, but special note might be made of the review of work on frost damage and its prevention and the valuable survey of the problems of strawberry growing provided by the East Malling strawberry team. The latter in itself is almost a complete guide to strawberry cultivation and ought to be read by every student and grower. Other papers deal with manurial experiments, plant injection as a diagnostic weapon, trials of the hybrid Rubi, and a survey of recent work on insecticides and fungicides.

Of the papers specially contributed to the volume, particular mention may be made of the survey of the present position with regard to the properties and uses of combined washes in the post-dormant spray programme, by Kearns and Martin. In view of the increase in cost of spray materials and the ever-increasing need for improvement in pest and disease control, the saving effected by the use of combined washes is assuming greater and greater importance, and the publication of an authoritative summary such as this is of much value.

Another paper of considerable interest is by Corbett on commercial rose-growing in glasshouses, while Miss Barton, of the Boyce Thompson Institute,

contributes a useful summary of the experiments at that institution on germination and dormancy of seeds. A short account of some preliminary trials on nutrient solution methods of growing plants is given by Mullard and Stoughton.

Continuing the policy of publishing regional surveys of horticulture, articles appear on horticulture in Eire, Devon, Lancashire and Bedfordshire, by the respective County Superintendents. An interesting account of the work of the Land Settlement Association, by Fairbank, concludes a volume which well maintains the standard of previous years. R.H.S.

STATISTICAL METHODS FOR RESEARCH WORKERS. By R. A. FISHER. Seventh Edition. (Oliver & Boyd, Edinburgh, 1938, pp. 356. 15s. net.)

Professor Fisher's first book now needs no introduction to horticultural research workers. Its appearance fourteen years ago occasioned something of a revolution in experimental methods, at first confined to the comparatively small world of biological science, but now spread to almost every field of scientific endeavour.

In the preface to the present edition the author reviews the additions and modifications which have been introduced in successive editions ; and indeed it is illuminating to turn back and compare the book which appeared in February 1925 with that now issued.

Much remains the same, but the hundred pages which have been added give only a small idea of the book's expansion, for the single chapter devoted to the Principles of Experimentation (Chap. VIII) had needed an entirely new volume, "The Design of Experiments" (Oliver & Boyd, 1935), to do it adequate justice.

To one who has endeavoured to follow the author since the earlier days, however, the most striking consideration is that, although the research problems, for the elucidation of which the statistician is called upon to find methods, become annually more complex, the methods themselves have actually been simplified. This fact is illustrated in this edition by the new and simplified approach to the theory of orthogonal polynomials. T.N.H.

DISEASES OF FRUITS AND HOPS. By H. WORMALD, D.Sc., A.R.C.S., D.I.C. (Crosby Lockwood & Son, Ltd., London, 1939, pp. 290. 17s. 6d.)

Although a considerable amount of research work has been carried out in recent years on the pests and diseases of fruits, much of it has been published in scientific or technical journals and is not easily accessible to the practical man or even to the horticultural advisory officer. As pest and disease control is so important an item in modern fruit-growing, however, there has for some time been a definite need for publications summarizing present knowledge, so that the most recent information would be readily available between two covers. Two members of the East Malling Research Station staff have now supplied this long-felt want and have thus conferred a double benefit on fruit-growers and advisory officers. Dr. Massee's book on the insect pests of fruits and hops is some two years old already ; now Dr. Wormald has produced what is, in many respects, a companion volume dealing with the fungus, bacterial and other diseases.

Dr. Wormald's book is planned so that information about any disease of fruit or hops can easily and rapidly be found. After three general chapters dealing respectively with Factors Conducive to Health or Disease in Plants, Fungicides and their Application, and Diseases affecting a Number of Host Plants (such as Crown Gall, Silver Leaf, Brown Rot, etc.), the remaining chapters deal with the diseases affecting the different types of fruit crops. In each chapter the diseases are grouped according to whether they affect the roots, stems and branches, leaves, flowers or fruit. The descriptions of individual diseases are so clear that recognition should be easy, and for each the appropriate control measures are briefly summarized. Dr. Wormald's long experience has enabled him to appraise very fairly the relative importance of the various diseases described, and this appreciably enhances the value of his notes. In most instances references to the more important research papers in English journals are added—a feature that will be valuable to advisory officers and research workers. Last, but not least, many of the diseases are illustrated in forty excellent plates that together must constitute one of the finest collections of illustrations of fruit diseases yet published.

Dr. Wormald's book is so good for what it is intended to be—a ready reference work to enable any fruit disease to be rapidly identified and the control measures ascertained—that a few criticisms seem almost out of place. The discussions of general principles in Chapters I and II contain many important ideas, but they are not always very fluently expressed or illustrated with concrete examples in a way that would make most appeal to the practical man. A number of sentences (such, for example, as the second sentence in Chapter II) are so overloaded with relative clauses and commas that they do not make easy reading.

Although "The Death" would seem to have been a very appropriate grower's term for a sudden dying of complete trees at a time when the cause of the trouble was still in doubt, it scarcely seems so appropriate for perpetuation in a book after the cause has been properly ascertained. It is always desirable that the common name of a non-parasitic disease should contain some indication of the cause of the trouble, if at all possible, and in this instance some such term as "Waterlogging Death" would seem to have been preferable for adoption in a book.

It is doubtful whether most of the "shot-hole" on peach leaves in this country, even on trees grown in the open, is due to the fungus *Clasterosporium carpophilum*, as is rather suggested on p. 157. This fungus has been definitely identified in England only on one or two occasions. Usually it is particularly difficult to determine the cause of shot-hole on peach leaves. The frequency with which the trouble is met on trees under glass suggests that it may be due more often than is supposed to the old explanation of the sun shining through drops of water on the leaves. Further information on the causes of shot-hole in peach leaves is therefore needed.

These, however, are very minor criticisms of a book which is packed full of information of value about the diseases of fruits and hops in England and which will be welcomed alike by the grower, the horticultural advisory officer and the research worker.

G.S.

THE INFLUENCE OF SIZE ON THE DRY MATTER, MINERAL AND NITROGEN CONTENT OF HYACINTH BULBS

By J. HARGRAVE and F. C. THOMPSON
The Agricultural Institute and Experimental Station, Kirton

INTRODUCTION.

ALTHOUGH on the Continent the bulb industry has been established for some two hundred years, in England it is only in the last twenty that any large scale development in the production of bulbs has taken place, although flower production, mainly from imported bulbs, has been established for a longer period.

The greater part of the experimental work carried out hitherto in connection with bulb growing has dealt with the cultural and morphological aspects of the subject ; very little purely chemical work seems to have been done with flowering bulbs.

In the United States, Nightingale and Robbins (1) have investigated the phases of nitrogen metabolism in the Paper White Narcissus, while in connection with storage problems, Moore (2), Pinkhof (3) and Algera (4) have studied the carbohydrate metabolism of tulips. Fondard and Gauthié (5), working on mineral composition, carried out a number of individual analyses of the resting organs of certain flowering plants, and similar estimations have been made by Handley and Hargrave (6) on varieties of hyacinths, tulips and Narcissi. The last-mentioned work deals mainly with single analyses of individual varieties, but no data appear to be available upon the variation in mineral composition of bulbs of any given variety in relation to their size.

It was therefore decided to investigate the variation in the dry matter, mineral and nitrogen content of different sizes of hyacinth bulbs, the variety L'Innocence being chosen for the purpose.

It was realized at the outset that it would be almost impossible to correlate age and size in bulbs chosen at random from a commercial stock, and it is intended, at a later date, to raise a stock of hyacinths wherein the age of every individual bulb will be known. It was considered, however, that valuable information might be obtained by considering size alone ; as soon as suitable material becomes available, the problem can be studied from the aspects of both size and age.

EXPERIMENTAL.

1. Materials and Sampling.

As already stated, bulbs of the variety L'Innocence were used for the investigation, and those selected had circumferences of 6, 8, 10, 12, 14 and 16 cm. respectively.

Six samples of each size were selected at random from a commercial stock of bulbs, propagated by the "scoop" method, and grown on the Institute Farm. The number of bulbs in each sample varied with their size as shown below:—

Size cm.	*Number.*	*Size cm.*	*Number.*
6	18	12	12
8	12	14	12
10	12	16	6

The bulbs were thoroughly cleaned and weighed on September 3rd, 1937. They were dried in a steam oven at 75-80° C. and ground in a coffee mill until a fine, even sample was obtained. The degree of fineness was such that approximately 60% of the material passed through an I.M.M. sieve, No. 60 (size of aperture 0·211 mm. sq.). The residual moisture was subsequently determined by drying at 105° C. for twenty-four hours.

2. Methods of Analysis.

Estimations were made of the following constituents:—nitrogen ; soluble ash ; potash (K_2O) ; phosphoric acid (P_2O_5) ; lime (CaO).

The modified Kjeldahl method developed by Ashton (7) for grass analysis was selected for the nitrogen determinations. The digestion is carried out in the presence of selenium, which greatly accelerates the clearing process.

The soluble ash figure was obtained by subtracting the weight of the material insoluble in boiling dilute hydrochloric acid from the weight of the total ash.

Potash was determined by the gravimetric cobaltinitrite method, using Hamid's (8) procedure. At the outset this method was checked against the perchlorate method, with satisfactory results. It was subsequently used in preference to the latter method, as it was found to be quicker and more convenient in operation.

Richards and Godden's (9) modification of the Pemberton-Neumann method was selected for the determination of phosphoric acid. After dissolving the ammonium phosphomolybdate precipitate in standard sodium hydroxide solution, the ammonia was removed by the addition of formaldehyde according to Scheffer's method, as described by Neumüller (10).

Calcium was determined by the A.O.A.C. (12) modification of McCrudden's (11) method. By this method the calcium is precipitated as oxalate under conditions which are more carefully controlled than by certain other methods in use.

DISCUSSION OF RESULTS.

The results of the chemical analyses together with those of analyses of variance for the different constituents are presented in Tables I-VII, and are illustrated by the graphs in text figures 1-3.

It will be realized that in preliminary work of this nature on a subject about which few experimental data are available, any conclusions drawn can

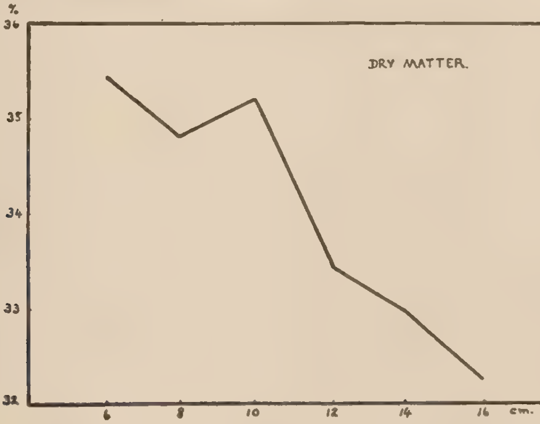


FIG. 1.
Mean Percentage Values of Dry Matter Contents.

be of a tentative nature only. Nevertheless, it is considered that the statistical results, allowing as they do to some extent for variation within each sample due to factors at present uninvestigated, afford some justification for concluding that in hyacinth bulbs size alone is one of the controlling factors in mineral composition.

DRY MATTER.

The bulbs appear to arrange themselves into two distinct groups. The 6, 8 and 10 cm. sizes, which form the first group, are all significantly higher in dry matter than the second, which contains the 12, 14 and 16 cm. sizes.

All the bulbs used had undergone the same storage treatment, as it is well known that such treatment may materially alter the moisture content of bulbs. Whether hyacinth bulbs of different sizes, under similar storage conditions, lose water at the same rate is a point upon which it has not been possible to obtain

TABLE I.

Chemical Data. Mean Values expressed as percentages of Dry Matter.

Size.	Dry Matter.	Nitrogen.	Soluble Ash.	Potash.	Phosphoric Acid.	Calcium Oxide.
6 cm. ..	35·42	0·840	2·639	0·920	0·399	0·479
8 cm. ..	34·81	0·827	2·471	0·828	0·352	0·451
10 cm. ..	35·21	0·930	2·680	0·896	0·368	0·430
12 cm. ..	33·42	0·920	2·728	1·073	0·392	0·468
14 cm. ..	32·98	0·907	2·790	1·046	0·383	0·439
16 cm. ..	32·24	0·979	2·980	1·150	0·434	0·436

TABLE II.

Analysis of Variance of per cent. Dry Matter Content.

Source of Variation.	Degrees of Freedom.	Sum of Squares.	Mean Square.	$Z=\frac{1}{2}$ ($\log_e$ Factor $-\log_e$ Error).	1% Points.	Significance.	Significant Differences.
Between Grades ..	5	51·6249	10·3250	1·0384	0·6540	Yes	6>12, 14, 16
Within Grades	30	38·8140	1·2938				8>12, 14, 16
							10>12, 14, 16
Total	35	90·4389					

TABLE III.

Analysis of Variance of per cent. Nitrogen in Dry Matter.

Source of Variation.	Degrees of Freedom.	Sum of Squares.	Mean Square.	$Z=\frac{1}{2}$ ($\log_e$ Factor $-\log_e$ Error).	1% Points.	Significance.	Significant Differences.
Between Grades ..	5	0·0986	0·0197	1·1691	0·6540	Yes	10>6, 8
Within Grades	30	0·0557	0·0019				12>6, 8
							14>6, 8
Total	35	0·1543					16>6, 8, 10, 12, 14

TABLE IV.

Analysis of Variance of per cent. Soluble Ash in Dry Matter.

Source of Variation.	Degrees of Freedom.	Sum of Squares.	Mean Square.	$Z = \frac{1}{2}$ ($\log_e$ Factor $- \log_e$ Error).	1% Points.	Significance.	Significant Differences.
Between Grades ..	5	0·9232	0·1846	1·1056	0·6540	Yes	12>8 14>8, 10 16>6, 8, 10, 12, 14
Within Grades	30	0·6090	0·0203				
Total	35	1·5322					

TABLE V.

Analysis of Variance of per cent. Potash in Dry Matter.

Source of Variation.	Degrees of Freedom.	Sum of Squares.	Mean Square.	$Z = \frac{1}{2}$ ($\log_e$ Factor $- \log_e$ Error).	1% Points.	Significance.	Significant Differences.
Between Grades ..	5	0·4503	0·0901	1·8698	0·6540	Yes	6>8 10>8 12>6, 8, 10 14>6, 8, 10 16>6, 8, 10, 12, 14
Within Grades	30	0·0643	0·0021				
Total	35	0·5146					

TABLE VI.

Analysis of Variance of per cent. Phosphoric Acid in Dry Matter.

Source of Variation.	Degrees of Freedom.	Sum of Squares.	Mean Square.	$Z=\frac{1}{2}$ ($\log_e$ Factor $-\log_e$ Error).	1% Points.	Significance.	Significant Differences.
Between Grades ..	5	0·0238	0·0048	1·1576	0·6540	Yes	6>8, 10
Within Grades	30	0·0140	0·0005				12>8
							14>8
Total	35	0·0378					16>6, 8, 10, 12, 14

TABLE VII.

Analysis of Variance of per cent. Calcium Oxide in Dry Matter.

Source of Variation.	Degrees of Freedom.	Sum of Squares.	Mean Square.	$Z=\frac{1}{2}$ ($\log_e$ Factor $-\log_e$ Error).	1% Points.	Significance.	Significant Differences.
Between Grades ..	5	0·0115	0·0023	1·3995	0·6540	Yes	6>8, 10, 14, 16
Within Grades	30	0·0042	0·0001				8>10, 14, 16
Total	35	0·0157					12>8, 10, 14, 16

any information ; and, although the variation would most likely be small, the possibility of the effect of an unknown factor of this nature must not be entirely dismissed.

ASH CONSTITUENTS AND NITROGEN.

The potash, phosphoric acid and nitrogen figures all show a fall from sizes 6 to 8, not significant, however, for nitrogen. Thereafter, all three show a general tendency to rise to a maximum. In all cases the 16 cm. size bulbs

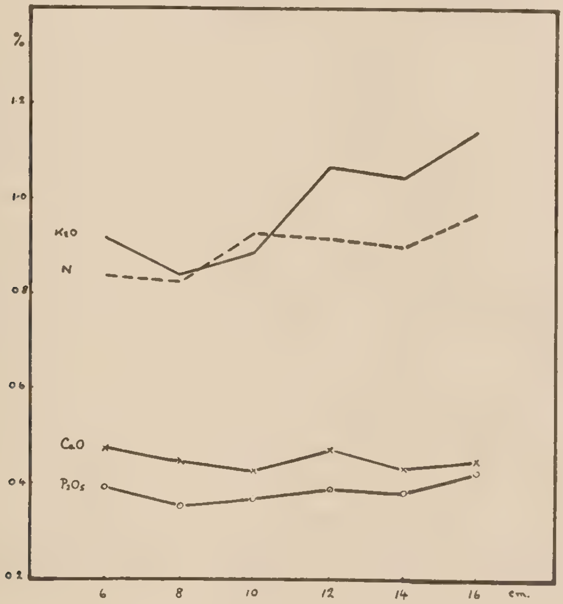


FIG. 2.

Mean Percentage Values of Nitrogen, Potash, Phosphoric Acid and Calcium Oxide Contents.

contain a significantly higher percentage of these constituents than do those of any other size. The rise after 8 cm. in all three groups may be connected with the increased capacity of the bulb for flower formation, root development and foliage production.

In the commercial production of bulbs the flowering head is removed at the time of full bloom and the foliage is allowed to die naturally, so that part of the nutrient material is transferred back to the bulb. Steele (13) states " that calcium, in contrast to potash and phosphoric acid, remains in tissues such as old leaves and is not withdrawn " ; if, therefore, the calcium is not returned, it is possible that the decrease found may be explained in this way. The sudden

rise in CaO content of the 12 cm. size is at present unaccountable ; it may perhaps be a chance result.

Bulbs of the 6 cm. size stand apart from the general rise, being more comparable in composition to those of the 16 cm. size except in regard to calcium content. The fact, however, that a bulb of this small size may be derived direct from the parent bulb as the result of one year's growth after propagation, may have some bearing on the matter. A bulb of this size has been able to draw upon the comparatively greater reserve of material stored in the parent, and the young bulb may have taken in a large amount of nutrient material as a foundation for its independent existence. In particular this may account for the higher percentage of calcium, which, as Steele (13) states, appears to be necessary for the growth of young root tissue.

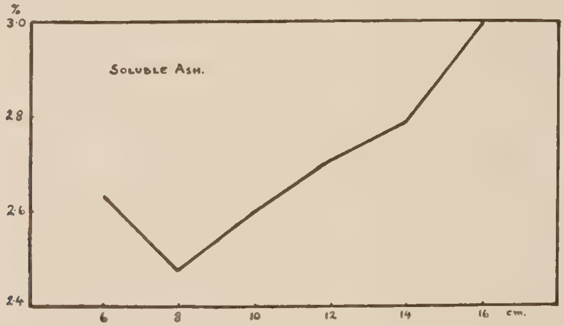


Fig. 3.

Mean Percentage Values of Soluble Ash Contents.

It is of interest to note that the analysis of L'Innocence bulbs of 16 cm. size made by Handley and Hargrave (6) shows a considerable measure of agreement with the figures given above for bulbs of that size.

Soluble Ash.

These figures, as might be expected, reflect the general tendency of rise and fall in the phosphoric acid and potash content, the greater percentages of these constituents appearing more than to outweigh any effect which might be shown by the decrease in calcium content.

Results on a Fresh Weight Basis.

It might be thought that the significant decrease in dry matter content, which takes place as the bulb increases in size, would counterbalance the corresponding increases in nitrogen, potash and phosphoric acid content, and that these results, when compared on a fresh weight basis, might show little or no differences

between sizes. In order to investigate this point, the results have been calculated on such a basis, and it has been found that significant differences still occur between the sizes, the general tendency being much the same as that from calculations made on a dry matter basis.

The differences between individual sizes, however, show a lack of consistency and are difficult to interpret. Furthermore, as stated above, though the bulbs were stored under identical conditions prior to analysis, the rate of loss of moisture may not have been the same in all sizes; in consequence, the figures stated in the customary way on a dry matter basis are likely to be more reliable.

Adequacy of Sampling.

From the tables of analysis of variance it will be seen that in all cases the variation is highly significant at the 1% point, from which it appears that the number of samples taken of each size was quite adequate for the purpose.

Additional Note on the Statistical Analysis.

A more comprehensive analysis of the variation between sizes has shown that for each constituent, a significant portion of the variation is due to a linear component, thus emphasizing the correlation between size and chemical composition.

ACKNOWLEDGMENTS.

The authors are indebted to their colleagues, Messrs. J. Wood and D. E. Horton, for helpful suggestions.

SUMMARY.

An investigation of the dry matter, mineral and nitrogen content of hyacinth bulbs ranging in size from 6 to 16 cm. is described.

Six random samples were taken in each size, to allow of statistical treatment of the results.

Differences were found to occur between sizes for all constituents examined, and their significance is discussed.

The results are given on a dry matter basis as being more reliable, although, when translated into terms of the fresh material, the general differences are still found in the main to hold good.

When due allowance is made for other sources of variation, the conclusion that size alone has a definite influence upon chemical composition appears to be justified.

REFERENCES.

(1) *Nightingale, G. T.* and *Robbins, W. R.* Some phases of nitrogen metabolism in polyanthus narcissus (Narcissus tazetta). New Jersey Agric. Exp. Sta. Bull. 472, 1928.

(2) *Moore, D. M.* Breaking the dormancy of tulip bulbs. Dissertation Ohio State Univ., Columbus, 1929. (Abst., Exp. Sta. Rec., 1932, **67**, 398.)

(3) *Pinkhof, M.* Untersuchungen über die Umfallkrankheit der Tulpen. Rec. Trav. bot. Néerl., 1929, **26**, 135.

(4) *Algera, L.* Concerning the influence of temperature treatment on the carbohydrate metabolism, the respiration and the morphological development of the tulip. Proc. Kon. Akad. v. Wet. Amsterdam, 1936, **39**, 846.

(5) *Fondard, L.* and *Gauthié, F.* Composition et exigences des bulbes fleurs en elements fertilisants. Internat. Cong. App. Chem., 1912, **15**, Sect. 7, p. 91.

(6) *Handley, F. W.* and *Hargrave, J.* Report on bulb experiments. The Agric. Inst. and Exp. Sta., Kirton, 1934-5.

(7) *Ashton, F. L.* Selenium as a catalyst in the Kjeldahl method as applied to soil and grass analysis. Journ. Agric. Sci., 1936, **26**, 239.

(8) *Hamid, M. A.* The determination of potassium in the presence and absence of sulphates. Analyst, 1926, **51**, 450.

(9) *Richards, M. B.* and *Godden, W.* The Pemberton-Neumann method for the estimation of phosphorus. Analyst, 1924, **49**, 565.

(10) *Neumüller, F.* Bericht über die Fortschritte der analytischen chemie. Ztschr. anal. Chem., 1935, **102**, 233.

(11) *McCrudden, F. H.* The quantitative separation of calcium and magnesium in the presence of phosphates and small amounts of iron devised especially for the analysis of foods, urine and faeces. Journ. Biol. Chem., 1910, **7**, 83.

(12) *Association of Official Agricultural Chemists.* Official and tentative methods of analysis. Washington, D.C., 1930.

(13) *Steele, C. C.* An introduction to plant biochemistry. London, 1934.

(*Received* 5/1/39.)

ON THE USE OF CHLORINATED NITROBENZENES FOR THE CONTROL OF CLUB ROOT DISEASE OF BRASSICAE

By MARGARET J. SMIETON
Biological Field Station of Imperial College of Science and Technology, Slough

INTRODUCTION.

WHILE it is generally accepted that the control of Club Root (*Plasmodiophora Brassicae*) on an agricultural scale is based on adequate crop rotation and on the application of lime, there is a demand for a directly fungicidal method of control, applicable at least on a horticultural scale. The use of lime has several disadvantages. It is often slow in action, it may be deleterious to some other crops, e.g. potatoes, and it has sometimes proved ineffective in controlling Club Root, even when sufficient is added to make the soil distinctly alkaline. Various mercurial compounds, organic and inorganic, have been tried in this connection, and the best evidence at present shows that mercuric chloride, applied in certain ways, gives a considerable measure of control (Preston (1, 2)). From a practical point of view the use of mercuric chloride has the serious disadvantage that owing to its extremely poisonous nature it is not readily obtainable by the grower and must be used with the utmost care. Furthermore, it has to be applied in solution, so that on a field scale large quantities of liquid have to be manipulated ; moreover, certain types of vessel cannot be used for it. A method which would avoid these difficulties would be welcome, and it was with this object that the work described in the present paper was undertaken. Experiments with chlorinated nitrobenzenes have been carried out over the past four years at the Biological Field Station, Slough, and sufficient evidence of their efficacy has now been obtained to warrant publication of the results.

MATERIALS AND METHODS.

The two substituted benzenes employed as fungicides, viz. pentachlornitrobenzene and trichlordinitrobenzene*, will be referred to throughout as Substances A and B respectively. Most of the work has been done with commercial preparations containing 20% by weight of the substances, but for special purposes the mixtures used have sometimes been compounded in the laboratory. Unless otherwise stated, the product used in experiments was the commercial one.

* These substances can be obtained in preparations under the trade names of " Folosan " and " Brassisan " respectively.

The two substances are available as fine powders, relatively insoluble in water. Fillers have been used to dilute them, such as finely divided slaked lime, chalk and talc ; these are indicated in brackets, e.g. Substance B (lime). The method of treatment with mercuric chloride described by Preston was adopted as a standard. The degree of disease control was assessed by recording the incidence of disease on the roots (numbers of visibly diseased roots and severity of clubbing), and by the effect on crop weight.

The efficiency of the substances has been tested in seed-boxes and in outdoor plots ; in the latter, applied both in the seed-bed and at the time of transplanting.

In the seed-boxes the fungicide was incorporated as evenly as possible with the whole bulk of soil. As the proportion of fungicide to soil was very small (usually 18 oz. to the cubic yard) the powder was first mixed with a small quantity of nearly dry, finely sifted, soil. For plot experiments, the fungicide (diluted with twice its weight of fine soil) was spread evenly over the area of soil to be treated, and raked or pricked into the top 3-4 inches. As a rule the seed was sown immediately after treatment.

The mercuric chloride solution was watered into the soil and it was necessary to allow the latter to dry for a few days before sowing. In all seed-bed trials the amount of seed used was weighed or measured for each row or each treatment. The method of treating the dibble holes at transplanting time will be described later.

Plots of ground naturally contaminated with the Club Root organism became available as the work proceeded, but at the start, and at various periods later, it was necessary to increase the supply by artificial contamination. All the soil for the seed-boxes was prepared in the latter way. For this, finely sifted debris from a rotted down pile of affected roots was intimately mixed with the soil some one to three or more weeks before use. For the contamination of outdoor plots, the infective material was spread evenly over the surface of the ground and worked into the top layer some weeks or months before the experiments were started.

Experience gained in the course of the work showed that uniform infectivity in different areas was very difficult to achieve. Even when the same amount of debris from the same pile was applied at the same time to different plots not far removed from each other, the degree of attack in the control rows sometimes showed great variation, so much so that some of the experiments were thereby spoilt. Presumably the cause of this variation lay in the heterogeneity of soil as between different plots. The difficulty was largely overcome by running the comparisons of the various treatments within the limits of one and the same plot. This unfortunately restricted the number of possible treatments, as the plots available were small (10 ft. × 10 ft.). The degree of attack in the controls on one and the same plot also varied considerably at different times of the year.

With seed-boxes, a fairly good degree of agreement among the various replicates was attainable by filling the boxes from the same heap of well mixed contaminated soil. The degree of attack in the controls in successive experiments was not uniform, but this was not altogether a disadvantage as it enabled an estimate of the efficiency of the various treatments to be made over a range of intensity of contamination.

Further details as to methods, arrangements of plots, etc., are given later.

EXPERIMENTS WITH SEED-BOXES.

These were carried out mainly during the winter in a heated greenhouse, their chief purpose being to compare the efficiencies of the two substances in powder form with that of mercuric chloride solution, and to gain some idea of the most promising dose suitable for outdoor experiments during the spring and summer. The results of an illustrative experiment are set out in Table I. The relevant details are as follows: The contaminated soil, after two weeks' incubation in a warm greenhouse, was divided into four parts and treated according to the scheme below, the mercuric chloride being watered over the soil after the boxes ($13{\cdot}5 \times 8{\cdot}5 \times 3$ in.) had been filled.

1.	Untreated	6 boxes.
2.	Substance A (lime filler), 18 oz. per cu. yd. ..	3 ,,
3.	,, B (,, ,,), ,, ,, ,, ,, ,, ..	3 ,,
4.	Mercuric chloride, 0·1% ; 2 gallons per sq. yd.	3 ,,

The dose of 18 oz. per cu. yd. was employed, since preliminary experiments had shown that when the contamination was not very severe, doses of Substance A of 12 oz., or even less, gave a very fair control, comparing favourably with mercuric chloride. Each box was sown with 2 grams of white mustard seed, this plant being chosen for its high susceptibility to Club Root and its comparatively short growing period. Seeding was dense so as to permit of sampling by thinning as the experiment proceeded. The average minimum and maximum temperatures of the greenhouse were 11·5° C. and 21° C. respectively.

None of the treatments caused any check to germination or growth, though a perceptible reduction in the stand of seedlings in two of the boxes treated with Substance B was noticed soon after germination. After six weeks, thirty seedlings were removed from each box, but traces of Club Root were found only in some from untreated boxes. A week later a varying amount of disease was found in all the controls, but none in any treated box. After another fortnight, i.e. sixty-one days after sowing, all the untreated boxes were examined, since "damping-off" was causing losses in some of them. At this date the amount of clubbing in plants from the treated boxes was very small,

TABLE I.

Treatment.	Box No.	Duration of experiment.	Number of plants.	Per centage clubbed.
Untreated	1	61 days	75	61
	2	,,	121	50
	3	,,	119	84
	4	,,	120	87
	5	,,	113	73
	6	,,	167	66
			Average ..	**70**
Substance A (lime filler) 18 oz. per cubic yd.	1	77 days	101	25
	2	,,	66	58
	3	,,	83	30
			Average ..	**38**
Substance B (lime filler) 18 oz. per cubic yd.	1	77 days	152	0
	2	,,	85	0
	3	,,	152	0
			Average ..	**0**
Mercuric chloride 0·1 per cent. solution	1	77 days	152	0
	2	,,	110	0
	3	,,	115	5
			Average ..	**2**

hence these were kept for a further sixteen days. Some damping-off occurred among these also. The final records are shown in Table I.

In this type of experiment the results have been examined statistically by calculating the value for "t" according to Fisher (3) for each treatment compared with the control, or between any two treatments, and finding the corresponding probability from the table. A value of $P = \cdot 05$ or less is taken to be significant. In the above experiment the almost complete control with Substance B and with mercuric chloride is obviously highly significant. When treatment with Substance A and the control are compared, the value for "t" is 2·985, and $P = \cdot 02$. The improvement is therefore clearly significant, though inferior to that shown by the other treatments.

The summarized results of the above experiment and of four others carried out on similar lines are assembled in Table II. These experiments include tests on the influence of various fillers and of the dose of Substance B.

The values for "t" and "P" are given in the last two columns for treatments compared with the control. The tests of significance for the effect exerted by the filler are as follows:—

Exp. II. Difference between lime and talc fillers for Substance A, $P = < \cdot 05$.
Exp. II. Difference between lime and talc fillers for Substance B, $P = < \cdot 01$.
Exp. III. Difference between lime and talc fillers for Substance B, $P = 0 \cdot 1 - 0 \cdot 2$.

The main conclusions to be drawn from these experiments are that Substance B is superior to Substance A, equalling mercuric chloride in two out

of three tests, and that lime is a more efficient filler than talc for both A and B. In the third experiment this difference is in the same direction though not in itself significant. As shown by Exp. III, a very small part (if any) of the control exercised by Substance B (lime filler) is due to the lime present. Under the conditions of Exp. IV, where an early examination was made on account of damping-off (chiefly in the untreated boxes), as low a dose as 6 oz. per cu. yd. of Substance B gave a high degree of control.

The only difference between experiments IA and IB, which were carried out simultaneously, was that in the latter the contaminated soil was stored under colder, outdoor, conditions before treatment and sowing. The degree of attack in the controls is seen to be markedly affected by this treatment, being greatly increased by the incubation at a higher temperature.

The foregoing experiments showed that a dose of 18 oz. per cu. yd. of

TABLE II.

Experiment.	Treatment.	Replications.	Mean % clubbed roots.	t.	P.
IA	Untreated	6	70		
	Substance A (lime filler)	3	38	2·98	almost ·02
	Substance B (lime filler)	3	0		
	Mercuric chloride	3	2		
IB	Untreated	3	36		
	Substance A (lime filler) ..	3	22	1·19	·3
	Mercuric chloride	3	2		
II	Untreated	6	96		
	Substance A (lime filler) ..	3	78	3·32	$<$·02
	,, ,, laboratory preparation	3	52	17·9	$<$·01
	,, (talc filler) ,,	3	76	4·19	$<$·01
	Substance B (chalk filler) ..	3	22	14·4	$<$·01
	,, (lime filler) laboratory preparation	3	24	29·8	$<$·01
	,, (talc filler) laboratory preparation	3	59	12·5	$<$·01
	Mercuric chloride	3	0		
III	Untreated	2	98		
	Substance B (lime filler) laboratory preparation	2	17	12·3	$<$·01
	,, (talc filler) laboratory preparation	2	50	4·36	almost ·05
	Lime alone equivalent quantity ..	2	89	3·40	$>$·05
	Talc alone ,, ,,	1	100		
IV	Untreated	2	78		
	Substance A (lime filler) ..	2	14		
	Substance B ,, ..	2	0		
	,, ,, $\frac{2}{3}$ dose	2	0·5		
	,, ,, $\frac{1}{3}$ dose	2	10		
	Mercuric chloride	2	1		

either powder was safe from the point of view of germination and subsequent growth. Substance A has always been found safe with various types of Brassicae at doses varying from 12 to 24 oz., and probably higher, and its use almost always results in a slightly increased percentage of germination. Mercuric chloride was harmless in these experiments on mustard, but it has on occasion caused some check or damage to young seedling Brassicas. In a test with higher doses of Substance B (lime filler), viz. 18-36-60 oz. per cu. yd., it was found that the 60 oz. dose somewhat reduced the germination of Shaw's Nonpareil cabbage and caused a persisting check ; the 36 oz. dose caused less check, which the seedlings outgrew ; while the 18 oz. dose showed little adverse effect at any time. The general conclusions from this part of the work are that Substance B (lime filler) at a dose of about 18 oz. per cu. yd. offers a promising control of Club Root. Substance A, which is somewhat safer from the point of view of plant growth, gives a more limited control.

TREATMENT OF OUTDOOR SEED BEDS.

The results obtained in the open have been irregular, some experiments having given a good measure of control and others much less. During 1935 only Substance A was tested ; in 1936 both powders were used, but the results were largely vitiated by poor germination and by the variation in disease intensity from plot to plot. Most of the data available relate to work carried out in the seasons 1937 and 1938.

The general method of treatment has already been described. The doses applied were at first based on the data obtained from the seed-box trials. The powders were applied at a given rate to the square yard, a dose of 12 oz. to the cu. yd. being equivalent to a surface dressing of 1 oz. to the sq. yd. worked in to a depth of three inches. The seedlings were examined when large enough for transplanting, and the numbers of clubbed and apparently perfectly healthy plants ascertained. The percentage of diseased plants would, of course, vary somewhat according to the date of examination.

A small scale experiment with Substance A (lime) in 1935 showed that doses of 1 and 1½ oz. per sq. yd. gave a very fair control in Purple Sprouting Broccoli and in Brussels Sprouts seedlings, during a period of seventy-eight days. The percentage of diseased plants in the controls averaged 66 and 65 respectively, and was reduced by treatment to mean percentages varying from 10-19. This degree of attack in the controls, though high, was considerably less than in some later experiments.

In the seasons 1936-38 the trials were on a larger scale, a number of contaminated plots (each 10 ft. × 10 ft.) being available. The method used was to divide each plot into 4 to 6 sections by sinking boards in them at

right angles to each other. Since the plots had proved to be so unevenly contaminated two control sections were included in each where possible, the remaining sections being subjected to the various treatments.

An experiment on these lines in 1937 provided information as to the behaviour of the fungicide under conditions of very variable contamination. The following treatments were given in four replicated plots which were sown immediately afterwards (April 29th) with Shaw's Nonpareil cabbage and a variety of broccoli:—

Untreated	2 sections per plot.
Substance B (lime filler), $1\frac{1}{2}$ oz. per sq. yd.	1 section ,, ,,
,, ,, ,, ,, 3 ,, ,, ,, ,,	1 ,, ,, ,,

The powder was worked into the soil by raking and subsequently pricking in with a fork to a depth of about 4 inches. In two of the plots symptoms of disease appeared early, the seedlings in the untreated sections being stunted. The experiment was concluded after 60 days when there was found to be a gradation amongst the plots from very severe to relatively slight attack. In the former, over 90% of the seedlings in the untreated sections had a root system consisting almost entirely of swollen main root clubbing. In this case neither treatment gave any useful control though the severity of attack (as judged by the degree to which the roots were affected) was somewhat reduced, and there was a very considerable increase in the weight of the plants from the treated soil, viz.:—

Weight calculated per 100 seedlings (cabbage):

Untreated	151 and 185 grams.
Substance B, $1\frac{1}{2}$ oz.	542 ,,
,, ,, 3 ,,	566 ,,

The results obtained from the two intermediately affected plots are given in Table III. Very small plants are not included in the figures.

As shown in the Table both treatments materially reduced the percentage of attack, in the less affected Plot II to almost negligible proportions. In view of some considerable variation between the two untreated sections in the plots, little reliance can be placed on the differential effect of the two treatments, since the difference is not marked and is not always in favour of the larger dose.

Both doses of the fungicide slightly checked early growth, but this effect soon disappeared. The same slight check occurred in another experiment started on 28/5/37, in which also there was often a considerable reduction in the number of seedlings in the treated sections (dose 2 oz. per sq. yd.). The weather at the latter date was much warmer than at the time of the first sowing, and no rain fell for a week after both sowings. Under warm dry conditions

the fungicide may be more harmful to germination, or the effect may have been due in part to drying of the surface soil by the process of incorporating the fungicide. This should certainly be avoided.

In the season 1938 a more elaborate test was carried out on a series of plots which included those used in the previous year. The top soil of the latter had in the meantime been removed, thoroughly intermixed so as to secure uniform contamination within each plot, and put back. Presumably on account of the unusually dry conditions in the spring and early summer, the incidence of disease was low. Considerable damage was, however, caused by cabbage root fly, and since there had been a suggestion in a previous year that this was increased by Substance A, attention was paid to this point.

TABLE III.

Plot.	Treatment.	Cabbage.		Broccoli.	
		Total No. of plants.	% clubbed.	Total No. of plants.	% clubbed.
I	Untreated (1)	229	95	111	96
	,, (2)	226	82	115	100
	Substance B, 1½ oz. per cu. yd. ..	242	46	130	35
	,, 3 oz. ,,	185	37	127	66
II	Untreated (1)	142	32	100	7
	,, (2)	194	58	132	46
	Substance B 1½ oz. per cu. yd. ..	157	6	127	7
	,, 3 oz. ,,	143	0	65	0

To ensure that any drying effects incidental to the incorporation of the fungicidal powders were equalized, all sections, including the controls, received similar surface cultivation.

The results obtained are summarized in Table IV, the first part of which shows the effect of a high dose of Substance B at two different dates of sowing (in the same plots) and of applying the fungicides a few weeks prior to sowing. The remainder deals with variations in the dose and filler of Substance B and with comparisons with mercuric chloride, lime and Substance A. The mercuric chloride and the lime were applied approximately two months before the date of sowing. Each experiment was carried out in quadruplicate.

Statistical analysis of the above results has been made and the following points are brought out:—

(a) Club Root occurred to a material extent in the first experiment only. In it very good control was obtained in the first sowing, and a significant ($P = < \cdot 05$, $< \cdot 01$) but less good one in the second. The fungicide gave much the same degree of control whether applied at once or some time before sowing.

TABLE IV.

Experiment.	Date of sowing.	Treatment.	Cabbage. var. Winnigstadt.			Broccoli. var. April Purity.		
			Average number of plants per plot.	% damaged by root fly.	% clubbed.	Average number of plants per plot.	% damaged by root fly.	% clubbed.
I	16.5.38	Untreated	161	14	27	185	6·5	30
		Substance B (lime), 3 oz. per sq. yd., at sowing	115	13·5	2	135	6	2
		,, ,, ,, 46 days before sowing	114	23	2	127	7	1·5
	1.6.38	Untreated	108	17·5	28	110	10	32
		Substance B (lime), 3 oz. per sq. yd., at sowing	65·5	47	2	59	29	10·5
		,, ,, ,, 16 days before sowing	56·5	36	8	54	16	9
II	20.5.38	Untreated (1)	140	16	9	163	8	10
		,, (2)	148	14·5	9	157	9	15
		Substance B (lime), laboratory preparation, 1½ oz. per sq. yd.	139	20	1	151	8	0·5
		,, (chalk), laboratory preparation, 1½ oz. per sq. yd.	135	24·5	1·5	157	9	3
		Substance A (lime), laboratory preparation, 1½ oz. per sq. yd.	130	23	0·5	149	12	1
		Mercuric chloride, 0·1% solution	173	3	0	183	0·5	0·2
III	28.5.38	Untreated	128	16	2	104	7	2·5
		Substance B (lime), 1½ oz. per sq. yd. ..	132	36	1	129	19·5	1
		,, ,, 3 oz. per sq. yd.	106	39·5	0·5	77	30	2
		Lime, 1 ton per acre	156	27	2	138	11	1
		,, ,, ,, + Substance B, 1½ oz. per sq. yd. ..	114	28	0	124	12·5	1
		Mercuric chloride, 0·1% solution	131	10	0	136	5	0

The difference between 2% and 8% in the second sowing of the cabbages was not significant. In the remaining two experiments the amount of Club Root in the untreated sections was too small to allow much value to be attached to the figures obtained.

(b) Considerable reduction in the stand of seedlings, varying from 25-50% was shown by the dose (3 oz. per sq. yd.) used in the first experiment, and this was larger in the later sowing, where also there was a reduced stand in the untreated sections. Rainfall and soil temperature records showed that in the ten days after sowing, only slight rain fell in both instances, but the average soil temperature was higher after the second sowing, thus confirming the suggestion previously made that phytocidal action is more liable to occur under warm dry conditions. The 3 oz. dose of Substance B which was repeated in Exp. III gave a non-significant decrease in the number of cabbage seedlings ; with broccoli there was a more pronounced decrease which was significant when compared with the other treatments, but not when compared with the control. In some instances treatment with Substance B caused a slight check to growth of the very young seedlings, but this soon disappeared as in the previous year.

(c) The figures for root fly infestation are irregular, but fifteen out of the twenty treatments with Substance B show a varying increase in the percentage of affected plants. Of these, however, the only examples which in themselves show a statistically significant increase are the $1\frac{1}{2}$ oz. and 3 oz. doses on cabbage and the 3 oz. dose on broccoli in Exp. III. Mercuric chloride, on the other hand, gave some control in Exp. II, and on cabbage in Exp. III, if compared with the Substance B treatments.

In so far as a comparison can be made between Substance B and mercuric chloride, the advantage is with the latter in respect of root fly control, and probably also of the stand of plants.

It is of interest that the germination of the seeds of certain weeds such as groundsel, shepherd's purse, fumitory, etc., was markedly repressed by Substance B, both in 1937 and 1938.

The evidence presented shows that under certain conditions where the disease is not unduly severe, Substance B, and also Substance A, so far as it was tested, control Club Root to a considerable extent. So far as comparisons can be drawn, mercuric chloride has shown itself to be the most effective of the substances tested. Substance B, under certain conditions at any rate, may reduce the stand of seedlings if used in greater amount than $1\frac{1}{2}$ oz. per sq. yd. It appears to be equally effective whether applied at the time of sowing or a few weeks before this, and it may safely be used on ground that has been limed.

TREATMENT AT THE TIME OF PLANTING OUT.

For these tests healthy plants were raised either in boxes of autoclaved soil or, when larger numbers were required, in ground where Club Root was not known to occur, this being heavily limed as an additional precaution.

The experiments extended over the seasons 1935-38, most of them being on plots that had been artificially contaminated in 1934 and 1935, which finally became very heavily contaminated. To a less extent some naturally contaminated land was also used. As already mentioned, uniformity of attack among the various plots was not achieved, so that (apart from the first year) each treatment was as far as possible included once or twice in each plot. The arrangement within the various plots was randomized. In one experiment, where a large piece of naturally contaminated land was available, it was possible to set out the plots in a Latin square.

In a few instances the fungicide was broadcast over the whole surface and raked or pricked into the upper 3-4 inches of soil. More often it was put directly into the dibble holes, a method which, if somewhat laborious, is economical of material. The fungicide was diluted with 3-10 volumes (in the different experiments) of nearly dry, sifted soil, and, as a rule, one level dessertspoonful of this mixture was applied to each dibble hole in such a way that it became distributed as much as possible on the walls of the hole. Planting followed immediately. The fungicides bulk somewhat differently according to the nature of the filler, so that when the effect of various fillers was being compared, certain adjustments in the proportions used had to be made. Soil is preferable to sand as a diluent since the latter tends to fall to the bottom of the hole.

As each experiment proceeded, observations on the presence or absence of a check to growth and on the appearance of Club Root symptoms, viz. blueing, wilting and arrest of growth, were made. With cabbages some experiments were ended by cutting the whole crop, weighing the tops and grading the roots with reference to severity of clubbing ; in others, the crop was cut as it matured. Since the plots were on a light sandy loam that had not been consistently manured, the general growth was rather poor ; and this effect was accentuated in some experiments by drought. The average plant weight, as given in the tables, is further reduced by the fact that all plants were included, whether they were mature or immature, and even if they were of a type which would never have headed at all. The method adopted was not one which would appeal to the practical grower, but is useful experimentally, since it provides data on the relative values of the treatments. With cauliflowers, the plants were cut and weighed as they matured.

The data from these experiments carried out in randomized blocks or Latin squares have been subjected to an analysis of variance (Fisher (3)). Where the numbers of plants in the control and treated plots are approximately

equal, or where a particular treatment can be shown to affect plant numbers, the analysis has been carried out on the total crop weight, in order to obtain the full value from the experiment. Where there are irregularities in numbers, due to accidental causes, the average weight per plant is taken as the basis of the calculation. The values for "t" with the corresponding probability "P" are given for each treatment compared with the control.

In 1935 an experiment was carried out in triplicate in which the following comparisons were made:—

(a) Untreated;
(b) Lime, 2 tons per acre;
(c) Substance A (lime filler), broadcast at 1½ oz. per sq. yd.;
(d) Substance A (lime filler), 1 level dessertspoonful of 1:3 mixture in dibble hole;
(e) Mercuric chloride, 0·05% solution, half-pint per hole.

Early London cauliflowers were planted throughout, and for treatments (a), (b) and (c) Wheeler's Imperial cabbage in addition. The experiment was interfered with by cabbage root fly, which affected all plots treated with Substance A very much more severely than the remainder. Without further evidence it is perhaps hardly safe to attribute the increased incidence of the pest to the treatment, but this was uniformly higher in each of the six plots in which Substance A was used.

The number of severely clubbed plants averaged 60% in the untreated plots for both crops, and all treatments markedly reduced this to mean values varying from 0% to 12%. The crop-weights showed great variation from plot to plot, and no significance could be attached to those for the cauliflowers. The increase in average weight of the cabbages, however, from 8 oz. (untreated) to 12 oz. (Substance A) and 14 oz. (lime) was highly significant ($P < \cdot 01$).

In 1936 Substances A and B were compared. As the plots of 1935 were again used, it was arranged that each treatment should be affected equally by any residual effect that might have persisted from the previous year.

Since Substance B was known to be more phytocidal than Substance A, a greater dilution was made with soil. Actually, in the first experiment, the dilution was somewhat greater than it appears, since the lime filler of Substance B bulks larger than the chalk filler of Substance A.

The treatments given were as follows:—

1. Untreated.
2. Substance A (chalk), 1:3 volume mixture; 1 level dessertspoonful per hole.
3. Substance B (lime), 1:5 volume mixture; 1 level dessertspoonful per hole.

Two rows of healthy young cabbage plants (Wheeler's Imperial) were planted on 27/5/36 under each treatment in each of six plots. Some check

was noticed in the treated rows. Five weeks after planting, from 5-10 of the 12 plants in each untreated row were seen to wilt in sunny weather, although at this time they equalled those in the treated rows in size. The latter showed no wilting except for one plant in a row treated with Substance A. During the next month the plants in the untreated rows made little growth and the improvement due to the treatments in the other rows became very pronounced. Just before cutting (12/8/36) the condition of the plants (64-66) under the various treatments was as follows:—

Untreated: Nearly all plants wilting or appearing blue.

Substance A: 5 wilted, 11 blue.

Substance B: 1 wilted.

The results of the final examination on 12/8/36 are given in Table V. Plants with roots showing only slight lateral attack are classed as healthy, since

TABLE V.

Treatment.	Number examined.	Number clubbed.			Weight of crop.	
		Very severe.	Medium.	Slight or healthy.	lb.	oz.
Untreated						
Plot 1	10	10	—	—	4	13
,, 2	12	12	—	—	2	8
,, 3	12	11	1	—	3	14
,, 4	10	10	—	—	0	13
,, 5	10	10	—	—	2	9
,, 6	10	10	—	—	2	12
Average	10·6	10·5	0·1	—	2	14
Substance A (chalk) 1 : 3						
Plot 1	11	11	—	—	11	11
,, 2	11	9	—	2	14	6
,, 3	12	10	1	1	11	15
,, 4	12	7	5	—	15	9
,, 5	8	6	2	—	9	12
,, 6	12	5	5	2	15	7
Average	11	8	2·1	0·8	13	2
Substance B (lime) 1 : 5						
Plot 1	9	4	4	1	21	3
,, 2	12	1	8	3	23	13
,, 3	11	3	7	1	15	14
,, 4	10	0	8	2	18	2
,, 5	11	1	9	1	25	4
,, 6	11	4	4	3	17	6
Average	10·6	2·1	6·6	1·8	20	4

Statistical analyses of weights:—

Untreated *v.* Substance A, $t=5{\cdot}86$, $P<{\cdot}01$.

Untreated *v.* Substance B, $t=9{\cdot}95$, $P<{\cdot}01$.

Substance A *v.* Substance B, $t=4{\cdot}08$, $P<{\cdot}01$.

that would have little effect on crop weight. In the column headed "Very severe" the root consisted almost entirely of a mass of clubbed tissue with no lateral growth at all. Examination of the roots of a number of plants that had previously been noted as wilting showed that they possessed hardly any fibrous roots. The growing season had been wet, otherwise many of the plants would have died, as occurred in the season following. From Table V it is seen that the disease in the controls was very severe; no marketable crop was produced. Although a high proportion of the plants treated with Substance B became attacked, the degree of attack was considerably reduced, and a fair crop was obtained. Substance A and Substance B gave crop weights which were respectively 4·5 and 7·0 times that of the controls. The improvement obtained by Substance B over Substance A was highly significant.

In a later planting (10/6/36) of the same variety of cabbage Substance A (chalk) was compared with two dilutions of Substance B (chalk) and with 0·05% mercuric chloride solution. Half a pint of the latter was applied to each hole before planting. The final examination was made on the same date as in the previous experiment, though some of the plants were not quite mature. The results from the four plots involved are summarized in Table VI. The disease

TABLE VI.

Treatment.	Number examined.	Number clubbed. Severe.	Medium.	Slight or healthy.	Weight average per plant.	t	P
					oz.		
Untreated	46	37	5	4	21		
Substance A (chalk) 1 : 3 ..	23	1	6	16	39	4·21	$<$·01
Substance B (chalk) 1 : 5 ..	23	1	1	21	34	3·12	$<$·02
Substance B (chalk) 1 : 9 ..	22	0	6	16	31	2·43	$<$·05
Mercuric chloride ·05% ..	24	0	1	23	29	1·97	$>$·05

in the controls was less severe than in the earlier experiments, since an average weight of 21 oz. as against 4 oz. was obtained, and observations in the field during growth supported this finding. Under these conditions all treatments gave good control of the disease with increases in crop weight. There was considerable variation between the replicates, but from the analysis of variance the treatment with Substance A gave an increase which was very significant; the increase due to Substance B was less but was also significant. It appears likely that some of the original check caused by mercuric chloride and, to a less extent by Substance B, persisted.

A further experiment in which the attack was so severe as to leave virtually no crop in the controls throws further light on the relative values of Substance A

(chalk) and Substance B (chalk), though neither gave an adequate disease control. The fungicides were broadcast at the rate of $1\frac{1}{2}$ oz. per sq. yd. All the plants in the untreated plots and in those treated with Substance A were severely affected, the average weights being 3·5 and 7·1 oz. respectively. Substance B caused some improvement, in that one-third of the plants were healthy or only slightly diseased, and the average weight was increased to 16 oz.

During 1937 and 1938 the standard method of dibble-hole treatment, viz. 1 level dessertspoonful of a 1 : 5 volume mixture of Substance B and soil, was compared with several modifications, with a view to overcoming the risk of a check due to treatment, or to economizing labour. The first results suggested that as far as disease control was concerned chalk as filler was at any rate not markedly inferior to lime, and that a dilution of 1 : 10 was effective. The results of five experiments in 1937 with Shaw's Nonpareil cabbage are given in Table VII. Some of the modifications tested are omitted from the table since they gave

TABLE VII.

Date of planting.	Treatment.	Number examined.	Number clubbed.			Average weight.
			Very severe.	Bad to medium.	Slight or healthy.	oz.
4.5.37	Untreated	21	20	1	0	0·9
	Substance B (lime) 1 : 5	21	0	21	0	6·8
4.6.37	Untreated	23	21	1	1	2·4
	Substance B (chalk) 1 : 10	23	11	10	2	13·0
4.6.37	Untreated	19	18	0	1	2·3
	Substance B (lime) 1 : 10	23	1	10	12	9·4
	Substance B (chalk) 1 : 10	24	2	14	8	12·7
18.6.37	Untreated	21	17	1	3	5·6
		24	16	6	2	3·7
	Substance B (lime) 1 : 10	24	0	9	15	14·0
	Substance B (lime) 1 : 5	23	0	8	15	11·2
	Substance B (chalk) 1 : 10	24	0	14	10	14·0
6.9.37	Untreated	30	27	1	2	4·0
		30	26	4	0	4·5
	Mercuric chloride ..	35	0	0	35	8·4
	Substance B (lime) 1 : 5	31	0	3	28	7·3
	Substance B (lime) 1 : 10	35	0	9	26	8·3
	Substance B (chalk) 1: 5	33	0	6	27	8·0

NOTE.—Adjustments were made in preparing the dilutions to compensate for differences in bulk between fillers.

TABLE VIII.

Date of planting.	Crop.	Treatment.	Number planted.	Number cut.	Average weight.	t	P	Number clubbed. Bad.	Medium.	Slight or healthy.
					lb. oz.					
10.6.38	CABBAGE (Shaw's Nonpareil)	Untreated	36	32	0 11	—	—	31	1	0
		Substance B* (lime) 1 : 5	36	29	2 0	4·65	<·01	3	19	7
		Substance B (chalk) 1 : 5	36	34	1 10	3·39	<·01	8	24	2
	SAVOY (Late Drumhead)	Untreated	72	68	1 3	—	—	37	22	9
		Substance B* (lime) 1 : 5	72	64	1 8	2·04	almost ·05	7	22	35
		Substance B (chalk) 1 : 5	72	67	1 9	2·42	<·05	4	36	27
28.6.38	SAVOY (Late Drumhead)	Untreated	54	52	1 0	—	—	46		6
		Substance B (lime) 1 : 5	54	44	1 6	1·32	<·3	24		20
		Substance B (lime) 1 : 5, above hole ..	54	48	1 8	1·81	<·1	27		21
		Substance B (lime) 150 oz. per cubic yd.†	54	51	1 4	0·91	<·4	25		26
		Substance B (lime) 300 oz. per cubic yd.†	54	47	1 5	1·28	<·3	19		28
		Mercuric chloride ·05%, ½ pint ..	54	53	2 2	4·12	<·01	7		46

* Laboratory preparations throughout.
† 100 cc. of mixture used to fill dibble hole.

inferior control. They are referred to in the following section. In the last experiment of the Table the crop was cut in April as spring greens before heading out. Disease was severe in the controls of all the experiments, and in the summer, crop yields were reduced by drought. All treatments gave a marked increase in crop weight and substantial disease control.

The results for 1938 are given in Table VIII. In the planting of June 28th, modifications of the treatment were included in which the standard dose was placed on the ground and the dibble hole made through it, or, a larger quantity of a more dilute mixture was used to fill the dibble hole. Because of drought it was necessary to water the earlier plantings. The later ones were not watered at any time and suffered severely from drought. This became obvious a few days after planting, since those treated with mercuric chloride solution became established before the controls, presumably on account of the moisture supplied by the treatment. Substance B caused a considerable early check in all cases, and this was more pronounced with the lime filler, especially with cabbage.

In the planting of June 10th, both treatments increased the average plant weight, more especially that of cabbage, though neither significantly affected the numbers or weight of crop which hearted. As before, the lime filler gave the better control of Club Root, the improvement being significant for cabbage and nearly so for Savoy. This result was confirmed in a later planting of Savoy, not included in the table.

In the planting of June 28th, mercuric chloride solution was superior to Substance B, partly no doubt for the reason given above. It significantly increased the number of plants that hearted, the average weight, and the number of healthy and nearly healthy plants, above those of the control or any other treatment. None of the treatments with Substance B gave a significant improvement except in Club Root control, in which respect all showed a considerable effect ($P < \cdot 01$). No differences were established between the various methods of applying Substance B. The method of filling the dibble hole with a large quantity of more diluted fungicide involves additional labour and is not sufficiently promising to warrant further testing. On the other hand, the method of laying the fungicide on the surface and passing the dibbler through it is worthy of further trial.

In an experiment begun on 9/6/37 and carried out on a piece of naturally contaminated land, two doses of a broadcast treatment and one dibble-hole treatment of Substance B (lime) were compared. It was possible to set out a Latin square, each plot measuring 10 ft. × 5 ft. The details of the experiment are given in Table IX. During July a slight check was noticed in some plots, particularly in those treated by the dibble-hole method, but the effect was not

consistent. By September the control plants appeared definitely poorer than the treated ones. Two cuttings of mature heads were made and the remainder, which would never have hearted, were cleared at the second date.

All three treatments much reduced the amount of disease, and approximately doubled the crop weight. This was true whether total or only hearted

TABLE IX.

Cabbage (Shaw's Nonpareil).

Treatment.	Plot.	Number examined.	Clubbing. Medium and very bad.	Clubbing. Slight or healthy.	Weight cut crop. lb.	oz.
Untreated	D3	17	12	5	10	2
	C4	13*	8	5	10	11
	B2	18	8	10	22	9
	A1	13	13	0	2	11
Average		15·2	10·2	5·0	11	8
Substance B (lime) broadcast, 1½ oz. per sq. yd.	D1	18	3	15	22	12
	C3	15*	3	12	21	8
	B4	18	1	17	23	5
	A2	18	5	13	24	6
Average		17·2	3	14·2	22	15
Substance B (lime) broadcast, 3 oz per sq. yd.	D4	18	1	17	15	6
	C2	15*	3	12	26	8
	B1	18	5	13	29	2
	A3	18	0	18	24	10
Average		17·2	2·2	15	23	15
Substance B (lime) dibble-hole treatment 1 : 10	D2	18	4	14	20	12
	C1	15*	2	13	25	0
	B3	18	4	14	22	13
	A4	17	0	17	15	15
Average		17	2·5	14·5	21	1

* 15 plants put out instead of 18, in error.

crop was considered. In spite of the uneven distribution of disease, which was well illustrated by the behaviour of the untreated plots, an analysis of variance carried out on the total weights of the plants showed that the increases due to all treatments were highly significant ($P = < \cdot 01$). There was no significant difference between the three treatments. It is of interest to note that the ground used had been limed in the previous year.

Broadcasting the fungicide, though promising, would be applicable on a commercial scale, only if it was applied to a small area around the plant, or drilled

along the row. A surface dressing of $1\frac{1}{2}$ oz. per sq. yd. would require 4 cwt. per acre, whereas if the fungicide is applied to the dibble hole as a 1:5 mixture with soil, 35-40 lb. will treat 10,000 plants.

The attempt to diminish the labour involved by the standard method of applying the fungicide to the dibble hole involved experiments on dipping the roots of the plants in a wet mixture of soil and fungicide before planting. Preliminary work in the greenhouse and in the open had shown that a mixture of 1:35 parts by volume was unsafe, hence greater dilutions, calculated on the basis of oz. to the cu. yd. were made. During the summer of 1937, when the disease was very severe, little control was obtained by doses which were,

TABLE X.

Treatment.	Number examined.	Number clubbed.			Weight.		
		Severe.	Medium.	Slight or healthy.	Average weight per plant.	t	P
					oz.		
Untreated	36	36	0	0	3·4		
Untreated—dipped wet soil	32	28	3	1	4·2		
Substance B (lime) 1 : 10	40	2	13	25	6·6	4·16	<·01
,, (chalk) 1 : 10	37	0	10	27	7·1	4·76	<·01
,, (chalk), dipped 250 oz.* ..	38	10	16	12	6·2	2·51	<·05
,, (chalk) dipped 350 oz. ..	37	5	8	24	4·8	0·83	>·4
,, (lime) dipped 250 oz. ..	42	9	22	11	6·0	2·36	<·05

* In wet mixture of 250 oz. fungicide to the cu. yd. of soil.

however, strong enough to cause an appreciable check to the young plants. In a planting made at the beginning of September the method was more successful. The cabbages (Shaw's Nonpareil) were cut as spring greens before they had hearted. The treatments and results are given in Table X. There was an early check with all treatments, but greatest with the 350 oz. dose (chalk filler). It is obvious that the Club Root control was not as efficient as with the dibble-hole method ; but with the exception of the 350 oz. dose, where the slight increase over the control weight was insignificant, the weights were nearly as high. It appears likely that the early check by the 350 oz. dose persisted. It may be remarked that in two other experiments, on clean soil, dipping the roots in 250 oz. mixtures did not give a noticeable check. It is possible, especially if further work could eliminate the danger of a check to growth, that a dipping method might, under certain conditions, such as obtain in autumn planting, give a useful measure of control.

CHECK TO GROWTH DUE TO TREATMENTS.

As will have been noted, in many of the experiments carried out, a check to growth was visible for some time at least after application of the fungicide. This check appears within a week or two, but unless pronounced it becomes less noticeable as time goes on. Whether it persists or not can be determined only by experiments on clean land, since on contaminated soil the controls which may appear to be in advance of the treated plants for some weeks, become affected by the disease later so that they finally lag behind.

Observations throughout the work have shown that often, but not always, some check to growth is produced by all three materials tested, Substance A, Substance B and mercuric chloride. The check with Substance A is definitely less than with Substance B ; as between the latter and mercuric chloride, the data are insufficient to determine which causes the greater check. The effect with Substance B often varies from plant to plant, some being definitely checked, others little or not at all. Mercuric chloride, on the other hand, tends to produce a more uniform type of check, all the plants in the batch showing it to much the same degree.

Within the limits of the doses tested, increased concentrations of Substance B do not always increase the degree of check, and conversely, in one experiment, a definite check was produced by a 1 : 19 mixture of Substance B (chalk), which was still visible after a month. Further, a given dose may at one time cause a check and at another time prove innocuous. This variability is probably associated with variations in soil factors (texture, moisture, temperature) and with the age and variety of the plants used ; but it is plausible to suppose that with the powders a large part of it is to be assigned to purely accidental circumstances, viz. the amount of fungicide which happens to adhere to the sides of the dibble hole. None of the broadcasting treatments has been found to give an appreciable check at any stage.

As illustrations of a permanent check the two following experiments may be quoted. In a small-scale planting of cauliflower (20 plants per treatment), Substance A (lime), 1 : 3, caused no delay in maturing, whereas Substance B (lime), in doses 1 : 3, 1 : 5 and 1 : 9, delayed maturity by about fourteen days.

During 1938, however, an experiment in which Club Root attack was negligible provided data on the permanence of the check. The season was very dry and all treatments caused a marked check soon after planting. Table XI gives the numbers and weights of Shaw's Nonpareil cabbage obtained from twelve randomized blocks.

The treatments had no appreciable effect on the numbers or average weight of the total crops, but both doses of Substance B significantly reduced the numbers of matured cabbages by 24-28% ($P = < \cdot 02$, $< \cdot 01$).

TABLE XI.

Treatment.	Number planted.	Matured crop. Number cut.	Matured crop. Average weight.	Total crop. Number cut.	Total crop. Average weight.	Total crop. Number clubbed.
			lb. oz.		lb. oz.	
Untreated	120	72	1 9	118	1 7	12
Mercuric chloride 0·085%	120	68	1 9	118	1 6	0
Substance B (lime) 1 : 5	120	53	1 10	111	1 5	0
,, ,, 1 : 10	120	55	1 13	116	1 7	6

The magnitude of the check produced by Substance B depends somewhat on the kind of filler used. Experiments both in the greenhouse and in the open have agreed in indicating that the check is greater with lime than with chalk or talc as filler (the last-named tested only in the greenhouse). Thus, in one greenhouse experiment, carried out in clean soil, the weight, after six weeks, of cauliflowers that had been treated by the dibble-hole method by Substance B (lime), 1:5, was on the average 27% less than the untreated ($P = < \cdot 05$) ; the same treatments with chalk and talc as fillers, and with lime alone in equivalent quantity, all gave an initial check which finally disappeared.

The foregoing comparisons were made with preparations compounded in the laboratory, so that the effects of the filler could strictly be compared. The outdoor experiments of 1937 bearing on this subject were made with commercial samples which are open to the objection that they may have been prepared from different batches of the effective constituent. These also agreed in showing that Substance B caused less check with chalk than with lime as filler. In spite of a somewhat reduced control of Club Root, the average plant weight was fully as great where chalk was the filler used (see Table VI). The actual differences in any one experiment were probably not significant, but the general tendency was in the direction stated.

In 1938, when laboratory preparations were used (see Table VIII), the same results were obtained as regards check, and the disease control was significantly greater where lime was the filler ; but this did not necessarily lead to a greater plant weight. The general conclusion is that the relative efficiency of the preparations and their final effect on plant weight depends very largely on the prevailing environmental conditions. Substance B with lime as filler causes a greater check in the early stages than with chalk, but also a greater degree of disease control. A check sometimes exerts a lasting effect. Mercuric chloride in general gives a more uniform check than Substance B, but a rather better control of disease, though not necessarily a greater final weight. There is no doubt that Substance B is more phytocidal in a dry than in a normal season. A small-scale planting of cabbages showed that this check was reduced by watering the plants in.

GENERAL CONCLUSIONS.

The results obtained may be summarized in the general statement that Substance B gives a substantial control of Club Root disease, sometimes, though not always, equalling that given by mercuric chloride. Substance A is definitely inferior from the point of view of disease control but is the least phytocidal of the three agents tried. Under conditions of relatively mild attack very good results have been obtained with Substance A.

It is probably true to say that in some of the experiments carried out, the conditions favouring infection were more severe than would be likely to occur often in practice. The ground had been artificially contaminated, and diseased crops had been grown in it for a number of years. Thus a higher measure of control might be expected under the more normal conditions prevailing in practice.

The first essential for the production of a good crop is the provision of healthy seedlings, and the experiments in this connection have been, on the whole, the least satisfactory. Again, the absence of visible clubbing at the time of transplanting is no guarantee that the seedlings are really free from infection. In fact, in one experiment with cauliflowers from seed-boxes, plants from a mercuric chloride treatment showed in the long run a heavy attack, though the percentage of infected roots was low at the time of transplanting. Here, again, the experimental conditions may have been too drastic. More cannot be said than that under a variety of conditions the use of Substance B, according to the methods described, has given an improvement—and in many cases a very substantial improvement ; but for its final evaluation, observations over a number of seasons and in a variety of naturally contaminated soils will be necessary.

ACKNOWLEDGMENTS.

The author wishes to thank Professor W. Brown for his interest and criticism throughout the work, and for his help in preparing the manuscript. She is also indebted to Dr. Lilian E. Hawker, who placed at her disposal information gained from early work carried out during 1934, particularly in relation to Substance A.

SUMMARY.

1. Pentachlornitrobenzene (Substance A), trichlordinitrobenzene (Substance B) and mercuric chloride were compared in seed-box experiments for the control of Club Root disease (*Plasmodiophora Brassicae*). Substance B sometimes equalled mercuric chloride in efficiency, and was superior to Substance A.

2. In outdoor seed-bed trials Substance B applied at the rate of $1\frac{1}{2}$ to 3 oz. per sq. yd. gave a varying degree of control depending upon the degree of soil contamination existing.

3. Substantial control of the disease, though not always equal to that given by mercuric chloride, was obtained by the addition of a small quantity of Substance B diluted with soil to the dibble hole at the time of transplanting.

4. All the substances tested are liable to produce a check to the growth of the plants, variable in intensity and persistence.

5. Various methods of applying the fungicides have been tested with a view to reducing the labour involved. A method of dipping the plant roots in a wet mixture of the fungicide with soil, previous to transplanting, has generally proved inferior to the standard dibble-hole method. Apart from the cost of application, promising results have been obtained by broadcasting the fungicide.

6. The fungicidal and phytocidal effects of Substances A and B were found to depend to a material extent on the particular filler used.

REFERENCES.

(1) *Preston, N. C.* Experiments on the control of finger-and-toe in cabbages. Welsh Journ. Agric., 1928, **4**, 280.

(2) ———. The prevention of finger-and-toe (Club Root) in gardens and allotments. Journ. Min. Agric. and Fish., 1931, **38**, 272.

(3) *Fisher, R. A.* Statistical methods for research workers. London. 1934.

(*Received* 14/2/39.)

DEVELOPMENTAL STUDIES IN THE APPLE FRUIT IN THE VARIETIES McINTOSH RED AND WAGENER

I. VASCULAR ANATOMY

By MARY MacARTHUR and R. H. WETMORE
Botanical Laboratories, Harvard University

A CHARACTERISTIC expression of heredity in an individual is the ultimate achievement of a specific form. This specificity of form is attained through the operation of a definite pattern of growth and development. An analysis of the ontogenetic evolution of the form may be placed on a cellular basis, for shape differences are measureable in terms of cellular activity ; that is, in distribution and duration of cell division, localization and duration of cell enlargement, and finally, volumetric increase of intercellular spaces. The present investigation was undertaken with the hope that a study of the structural framework and the internal organization of all the tissues, and the cellular changes in those tissues throughout the developmental history of the organ, might give some understanding of how the dynamic forces of heredity express themselves materially in that organ. A complex fruit—the apple—was chosen for this study, (1) because of the availability of material which satisfied the necessary biological requirements, (2) because of a hope that such a developmental study might provide new information bearing on the controversial nature of the apple fruit, and (3) because of the desire to apply such developmental studies to a possible examination of the supposed phenomenon—metaxenia.

Fruits utilized in an investigation of this sort must satisfy certain biological requirements ; e.g. (1) they must have easily discernible shape differences ; (2) they must be from plants with the same chromosome number ; (3) they must be from plants which are at least somewhat self-compatible ; (4) they must be from flowers whose pollen and stigmas ripen at about the same time, permitting reciprocal pollination on the same day ; (5) they must require about the same interval of time for growth and maturation ; and (6) the plants bearing them must be approximately of the same age and must be grown under the same nutritional treatment.

For these reasons the fruits of the apple varieties McIntosh Red and Wagener were chosen. The mature McIntosh apple is quite uniform in shape, the angulation is very faint, and the stamens are basal to median in their position

on the basin*. The Wagener is unequal-sided, definitely angulated, particularly at the apex, and the stamens are attached to the basin higher up than in the McIntosh. The somatic chromosome number of each is thirty-four. They are inter-fertile, and somewhat self-compatible. They bloom at approximately the same time, and the time required for growth and maturation of the fruits is about the same for both varieties. It is recognized that both of these apple varieties are heterozygous. Inasmuch as this investigation was developmental in nature and confined to a study of fruits from two different trees, it was felt that the heterozygosity factor need not be taken into consideration.

The first and necessary step in a study of this sort is a comparison of the structural frameworks of the two varieties. Therefore, the first paper will deal with a comparison of the vascular anatomy.

MATERIALS AND METHODS.

In 1935 collections were made from two adjacent trees of McIntosh and Wagener varieties of apple at the Dominion Experimental Farm, Kentville, Nova Scotia, Canada. These trees are in the same nutritional plot. They are subjected to the same environment in so far as environment can be controlled. Branches were isolated by covering them with cheesecloth. The earlier blooming terminal flower of each cluster was removed. When the stigmas were ripe the flowers were pollinated by hand. To obtain a high percentage of set in the McIntosh, a variety in which self-compatibility is low, the stigmas were brushed immediately before pollination with a 15% sucrose solution, a percentage which has been productive of good results in this orchard.

Collections were made at irregular intervals until the reciprocal pollinations were effected on June 8th. Daily collections were made on the ten days succeeding pollination. From that time until the maturity of the fruits, collections were made so far as possible at least once a week in the younger stages, then twice a week. Unfortunately, the set in McIntosh was too low to provide a complete collection of the later stages. Additional earlier and later collections were made in 1936.

All collections except the mature apples were fixed in the Allen-Wilson modification of Bouin's solution. Those younger stages which were to be sectioned with the microtome were given a short period of treatment in hydrofluoric acid (Bonne (1)) to remove the numerous crystals of calcium oxalate in the carpellary region. After washing in water, this material—up to 2 cm. in diameter—was carried through a modified form of Zirkle's (16) butyl series and embedded in paraffin. At the 75% butyl, 25% ethyl stage, the buds were

* The term " basin " is used to describe the depression at the distal end of the fruit; the term " cavity " that part of the fruit bearing the stem.

carefully scraped with an iridectomy scalpel, to remove the thick coating of unicellular sclerified hairs which interfered with the cutting.

Transverse and longitudinal serial sections, 10μ in thickness, were made. Of the stains tried, a triple stain of haematoxylin, crystal violet and orange "G" proved the most satisfactory. Thinly sliced median sections of the larger material were cleared using a modification of Kraus's (7) clearing method.

By means of the Edinger apparatus, drawings were made of those sections in a series showing the salient points necessary for the building up of the complete vascular picture. Comparable sections of later collections were checked with those of the earlier for changes and similarities.

OBSERVATIONS.

The fundamental vascular pattern is the same for both varieties. This general vascular pattern will be described and the varietal differences pointed out.

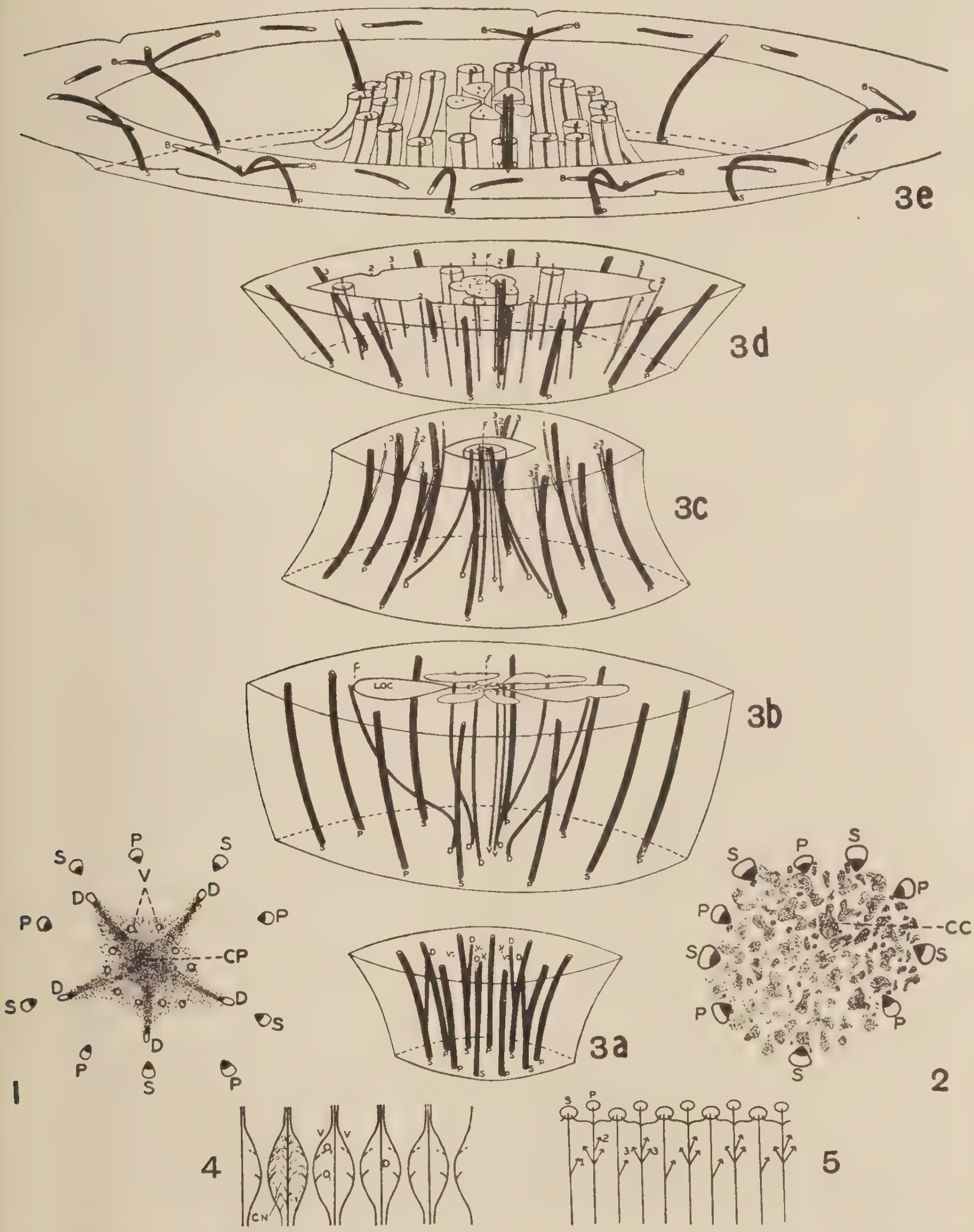
A. Pedicel.

At the base of the pedicel there are five large bundles arranged in a rough pentagon. A number of smaller bundles alternate with the larger ones rounding out the pentagon into an irregular cylinder. This is in accordance with the observations of Kraus and Ralston (9). The bundles of the pedicel are separated by cells similar to those of the pith and cortex except that they are elongated radially. Pericyclic caps limit each bundle on its outer face. The lignification of the bundle caps fades out at the point where the bundles diverge into the cortical tissue. In many cases two bracts are attached to a pedicel (Pl. II, Fig. 1). The lower one may be attached near the pedicel base or higher, while the second is attached on the opposite side near the mid-region of the pedicel. Each bract is supplied by one bundle.*

Generally, between the mid-region and the summit of the pedicel, the five main bundles divide radially as the smaller bundles move in from the cylinder to the pith (Pl. I, Fig. 2). These main bundles do not all divide at the same level, but at that point near the pedicel apex where the bud begins to flare out they have completed their radial division. Up to this point no branches or bundles other than those bracteary bundles mentioned above pass outward from the sides of the ten bundles. The ten bundles shortly become arranged to form the outline of a fluted cylinder. This cylinder is the periantho-staminal complex. The five outer bundles are the sepal bundles, for the distal termination of each is in a calyx lobe. In the same way the inner five bundles of the cylinder may be termed the petal bundles. Internal to the periantho-staminal cylinder there are numerous small bundles termed here the *central complex* which will be dealt with under the carpellary system (page 224).

* Note single bundle in lower part of figure, Plate II, Fig. 1. Upper single bundle not so clearly shown because of surrounding parenchyma.

PLATE I.



IG. 1. Diagram showing the vascular system of the apple fruit at level of Fig. 3a, top. S, sepal bundle; P, petal bundle; D, dorsal carpel bundle; V, ventral carpel bundle; CP, central parenchyma.

G. 2. Diagram showing the vascular system of the apple fruit near the apex of the pedicel. CC, central complex.

G. 3a-3e. Diagram showing the vascular system of the apple fruit. Loc, locule; C, protuberance of tissue into locule opposite dorsal carpel bundle; F, central cavity (stylar canal); 1, 2, 3, stamen bundles; B, branch of petal bundle to calyx lobe.

G. 4. Diagram showing vascular supply of the carpels. O_1, O_2, ovular traces; CN, carpellary network.

IG. 5. Diagram of the periantho-staminal vascularization. S, sepal; P, petal; 1, 2, 3, stamen traces.

Along the pedicel at that level where the cortical tissue becomes more extensive, each sepal bundle gives rise by radial division to a dorsal carpel bundle (page 225). From this point the ten primary bundles follow a gradual upward and outward course.

B. Periantho-Staminal Bundles.

At the pedicel apex the ten primaries radiate outward sharply, like the spokes from the hub of a wheel. This orientation is noted in immature fruits. In mature fruits they may be curved downward slightly, while in buds and very young fruits (Pl. I, Figs. 3a, 3b) they outline the form of a cone. In all cases the primary bundles finally bend around the carpels and ascend at some distance from them (Pl. I, Fig. 3b). They follow a course which marks the line of division between pith and cortical tissue.

1. *Cortical Vascular System.*

In the lower part of the fruit small secondary branches separate from the primaries and diverge outward and upward into the cortex. From the point of great divergence of the ten primaries, larger secondary bundles are given off to the cortex. The course of these latter bundles is, in general, outward and downward (Pl. III, Fig. 4). As the primaries ascend, still other secondaries arise and pass outward and upward.

In the Wagener variety these secondaries are generally given off in pairs of nearly equal size (Pl. III, Fig. 1). They swing away from the main bundle in arcs, to the right and to the left respectively. This uniformity of size and regularity of course is a contributory factor in the formation of the roundly-lobed appearance of the dividing line between pith and cortex so plainly seen in median transverse sections of the mature fruit (Pl. III, Fig. 1). However, this line of division is mainly an area of somewhat smaller cells, with smaller intercellular spaces, with irregular orientation and with a different staining reaction of the cell contents from those of the cortex. In buds and very young fruits these differences are not marked.

No such regularity of branching is found in the McIntosh variety. Secondaries are not generally paired, or if paired, they are of unequal size. Their course is more or less angular. Median transverse sections exhibit an angular appearance of the dividing line between pith and cortex (Pl. III, Fig. 2). This angularity has been described in the McIntosh by Kraus (8). According to Tetley (13) it is a line of cells, transitional in type between those of the cortex and the pith, resulting from differential strains to which they are subjected. Kraus considered that the line marked a region of cambial activity. Neither Tetley nor the present writers have found evidence of a cambium here. Near the apices of the loculi the primaries arch inward (Pl. I. Fig. 3c), still following the carpel outline and at about the same distance from it.

The secondaries from the sepal and petal bundles ramify through the cortex, forming the outer network. Subdivisions occur in profusion in the external cortical tissue. Smaller branches also arise from the primaries and may subdivide at a greater or less distance from them, or may not branch at all. In this case they terminate generally in the sub-epidermal tissue as one to several long, narrow, parenchymatous cells. As the outer cortex is approached, anastomoses occur between the finer ramifications (Pl. III, Figs. 1-4). This is the "reticulum" of the Yellow Newtown variety, investigated by Kraus and Ralston (9), and the "système vasculaire périphérique" of Bonne (1). In no case does the cortical network extend into the epidermis.

In the McIntosh the reticulum is much more extensive than in the Wagener; that is, bifurcations and anastomoses are more numerous and the cross-sectional diameters of the reticular threads are, in general, greater in the former than in the latter.

2. *Origin of Stamen Bundles.*

The first staminal bundles to arise (Pl. I, Fig. 3c, 1, and Pl. I, Fig. 5, 1) have their origin in the outer five primaries (the sepal bundles). In the McIntosh, the division generally occurs at a level below the apex of the locule. In the Wagener they are given off at a higher level, near or at the bottom of the basin. These staminal bundles, the protoxylem of which is continuous with that of the sepal primaries, follow an inward and upward course. They enter the filaments of the *inner* circle of five stamens (Pl. I, Fig. 3d, 1) near the middle of the basin in the McIntosh (Pl. III, Fig. 4), but at a slightly higher point in the Wagener (Pl. III, Fig. 3). Each stamen of this circle is directly in front of, and lower than, the median bundle of a calyx lobe. All staminal bundles are concentric. At a higher level than the origin of the first staminal bundles, and correspondingly higher in the Wagener than in the McIntosh, the *petal* primaries give rise to two staminal bundles one on each side of the protoxylem ridge (Pl. I, Fig. 3c, 3, and Pl. I, Fig. 5, 3). As with the first series, these swing upward and inward, diverge laterally and terminate in the outer or third circle of stamens (Pl. I, Fig. 3e, 3). The lateral divergence of these pairs carries them to a position, one to the left, one to the right, and slightly distal to the stamens of the first circle. The same primaries (inner, or petal bundles), at a point slightly above the separation of the paired staminal branches, give rise to a third series of stamen bundles (Pl. I, Fig. 3c, 2, and Pl. I, Fig. 5, 2). These arch inward and upward, midway between the laterally divergent pairs. They terminate in the stamens of the middle or second circle (Pl. I, Fig. 3e, 2). Each stamen of this circle is directly in front of, and slightly below, a petal. Thus, in a normal apple there are twenty stamens grouped into three circles—an inner circle of five, a median of five, and an outer of ten.

3. *Petal and Sepal Bundles.*

Above the point at which the last stamen bundles arise, and where the primaries are again arching definitely outwards, two more branches depart from each petal bundle, one to the right, one to the left respectively (Pl. I, Fig. 5). These diverge sharply while the main bundle changes from an outward to an upward direction, and enters the base of the petal as a single flattened bundle. It continues to the slightly notched, distal end of the petal, bifurcating beneath the notch. The petal is pinnately veined. The secondaries from the main bundle branch and rebranch to form the familiar netted venation of the apple petal.

The last two bundles (Pl. I, Fig. 3e, B), diverging sharply from the petal primary, approach the right and left sepal primaries by swinging in a right and left arc, respectively, below the notch between two calyx lobes. Thus, there are entering each calyx lobe three bundles, a median, a right and a left. The median is the continuation of the sepal primary. The right and left are from the petal primaries to the right and left respectively. These last two bundles are slightly smaller than the sepal primary at this level, and after entering the sepal they quickly diverge from the sepal primary. The three bundles then give off numerous branches to form the vascular system of the net-veined calyx lobe, the primary itself ending beneath the tip.

The only branches originating in the primaries to follow an *inward* course are the median carpellary bundles at the base of the fruit and the staminal bundles at the apex. All other branches extend into the cortex ; but a cortical branch may swing in toward the pith, and after a short distance, arch outward again.

C. Carpellary System.

1. *Origin of Carpel Bundles.*

Half-way up the pedicel several very small bundles move in towards the pith. These may be several of the smaller bundles of the pedicel (page 220), or they may arise by anticlinal division of the five main bundles. This complex comes to form a dense anastomosis of bundles. In the bud, however, these bundles may be wholly or mainly procambial. Often the group of cells, numbering ten to twelve, which constitute one of these small inner bundles, occupies no greater area in transverse section than that of a single pith cell. Even below the point at which the bundles move in from the pedicellar cylinder to form the central complex, some few small bundles are observed in the pith. A careful examination of the serial sections shows that these bundles, ending blindly, are downward prolongations of that dense anastomosis of bundles just referred to, which ramifies through the pith in the upper part of the pedicel (page 222).

Between the mid-region and the summit of the pedicel the remaining small bundles of the pedicel circle also move in towards the pith, and anastomose with those mentioned above. These bundles are diversely oriented. Some of the larger bundles in this central complex (Pl. I, Fig. 2, CC) have small caps of cells similar to those of the pericycle of the pedicel cylinder. The vascular cylinder of the pedicel now consists of five to ten primary bundles—the number increasing from five to ten as the main bundles divide anticlinally to form the ten primaries (page 220)—and, internal to the primaries, the central complex (page 222), a central cylinder of anastomosing bundles.

In fruits collected on July 11th, the majority of the pith cells have changed to stone cells, but some few have remained parenchymatous. At this time the apple is increasing enormously in size, and the fruits have become pendulous.

At that point along the pedicel where the cortical tissue becomes more extensive, five bundles originate (page 222) through unequal radial dichotomies of the sepal bundles. Each smaller bundle resulting from these radial divisions swings in towards the pith, and orients itself in a position directly in front of its sepal bundle and between it and the central complex. These five smaller bundles are the dorsal or median carpellary bundles (Pl. I, Fig. 1, D). It is important to note at this point that there is no further radial division of the primary bundles. The dorsal carpellary bundles on passing in towards the pith may, or may not, "fuse" with the bundles of the central complex. In the Wagener, they generally remain distinct, while in the McIntosh, "fusion" occurs more often. Immediately above the separation of the dorsal carpellary bundles from the sepal primaries, the inner complex resolves itself into ten bundles arranged into five pairs on the circumference of the central region (Pl. I, Fig. 1, V). Some few small bundles and much parenchyma occupy this central region. External to the five pairs of bundles, and forming with them a five-pointed star, are the dorsal carpellary bundles (Pl. I, Fig. 1, D). The paired bundles are the ventral carpellary bundles. Of these pairs, one bundle serves the carpel to the right, the other the carpel to the left. The pairs are situated at the inner angles of the star. The remaining small bundles in the central complex unite with the ventral bundles before the bases of the locules are reached. Therefore, when the bases of the locules are reached, the carpellary system is composed of five dorsal bundles and ten ventral bundles.

In the bud, the xylem elements are few in the dorsal carpel trace and still fewer in the ventral traces. With growth of the fruit, the conducting tissue in the dorsal trace increases. In older fruits the xylem elements of the ventral traces increase in number enormously, particularly if the ventrals serve fertilized ovules. Should the ovule become aborted after fertilization, the ventral trace serving it becomes more or less disintegrated. In such cases the tracheids

remain distinct, while the parenchyma and the phloem of the bundle collapse and disintegrate, leaving lacunae.

2. *Course of Carpel Bundles.*

At the apex of the pedicel the dorsal traces arch outward, then obliquely upward to follow the dorsal sutures of the bi-partite loculi (Pl. I, Fig. 3b, D). As a dorsal trace approaches the apex of a locule, it swings inward again (Pl. I, Fig. 3c, D), and passes up the five-partite style to end beneath the stigma of one of the stylar branches.

At the base of the locule the ventral bundles (Pl. I, Fig. 3b, V) may be either concentric or inverted. In inverted bundles the xylem is on that side facing the locule. Occasionally in the Wagener, and more often in the McIntosh, pairs of adjacent ventral bundles unite by their phloem faces to form one bundle. It is of interest to note that Grew (4) reported a circle of five placentary bundles. The bundle serving adjacent carpels may become concentric as the xylem moves towards the centre and the phloem moves to a peripheral location. The ventral bundles continue to the apices of the loculi, decreasing in diameter from the mid-carpellary region to the apex, and pass up into the style to end as do the dorsal bundles, beneath the stigmas. The continuance of the dorsal and the two ventral bundles to a point immediately beneath the stigma suggests Hunt's Type 2 in carpel development (6). In passing up the style there is an increase of peripheral parenchyma in both dorsal and ventral bundles.

3. *Carpellary Network.*

Throughout the region of the locules, branches are given off by both ventral and dorsal bundles. A pair of these, arising from the ventrals of each carpel at or near the mid-region of the locule, are ovular traces (Pl. I, Fig. 4, O_1). Other such pairs may take their departure from the ventrals between the mid-region and the summit of the locule. These latter pairs (Pl. I, Fig. 4, O_2) supply the supernumary ovules (page 000). All other branches arising from the ventral and dorsal bundles form a network in the carpellary projections between the loculi (Pl. III, Figs. 1-4). Median transverse sections of McIntosh show that this network closely follows the outlines of the locule (Pl. III, Fig. 2). In the Wagener, the outline flares out at the sides of the locule, and is truncated in the region of the dorsal bundle (Pl. III, Fig. 1). Small branches may run a short distance into the pith, and other branches may extend from the dorsal carpel bundles almost to the sepal bundle.

4. *Formation of "Open" or "Closed" Core.*

A transverse section of the style just above the base of the apical depression or basin shows it to be five-partite (Pl. I, Fig. 3d). The contour of the pistil is lobed. Internally there is an elongated star-shaped opening, the stylar canal

(Pl. I, Fig. 3d, F). Each point of the star extends towards a notch in the pistil outline. Nearer the distal end, the extension of the star-shaped fissure completely divides the pistil into five carpels. The inner edge of each carpel shows an infolding, also noted by Kraus (7). This fold may be followed down to the base of the locule and is generally interpreted as the "fusion" of the ventral edges of the carpels.

In young buds, before the ovules appear, the carpellary region is completely open towards the centre (Pl. II. Fig. 2). With further growth, the basal cushion of parenchyma is elevated ; the ventral lobes of continuous carpels grow centripetally. In the Wagener this centripetal growth, coincident with the infolding of the ventral edges of the carpels, completely blocks off the loculi and leaves the central star-shaped opening. Thus the core of the Wagener is "closed" (Pl. II, Fig. 4) ; that is, there are no openings from the central cavity into the locules. The central cavity is not an ovary. It is formed by the failure of the ventral lobes of the carpels to continue their initial centripetal growth to form a solid central core. This cavity is lined with epidermis, and the occasional extension of an epidermal cell to form a unicellular hair, similar to those coating the upper part of the pistil, may be seen. In the McIntosh, centripetal growth is delayed ; the ventral edges of the carpels do not "fuse" as in the Wagener. Thus the loculi remain open into the central cavity (Pl. II, Fig. 3). Although in the mid-carpellary region this central cavity is larger in the McIntosh than in the Wagener, upon its continuation through the style as the stylar canal, its diameter decreases to nearly zero. In the Wagener the stylar canal has a greater diameter.

5. *Orientation of Ovules.*

The ovules appear very early in the development of the bud as small protuberances on the placentae, about half way up the locule. Later in ontogeny the integuments appear, and at the same time the megaspore mother cell is seen in the nucellus. At the time of anthesis, the integuments completely cover the nucellus, leaving only the micropylar opening. The anatropous ovule eventually comes to rest with the micropyle in close proximity to the obturator, a small irregular pad of placental tissue at the base of the funiculus. In the Wagener the ovule swings through a vertical angle of 90° to assume its anatropous position. At the same time it comes to lie close to that side of the locular wall to which it is attached. Thus the ovule becomes oriented *longitudinally* in that half of the bi-partite locule supplied by its ventral trace. Wagener shows regularity in the pairing and orientation of the ovules (Pl. II, Fig. 4). In most cases there are ten ovules in five pairs of two, one pair to each carpel (page 226). Some fruits, particularly in the younger stages, may have two pairs of ovules per carpel, or three ovules per carpel. In such cases the extra ovules are supplied

by ovular traces given off from the ventral traces at a point between the mid-region and the apex of the locule (Pl. I, Fig. 4, O_2). In older fruits of Wagener the number is greatly reduced, due to the abortion of certain of them. Sections through this region show these aborted ovules as dark staining areas still attached to the placentae. Examination of mature fruits discloses them as tiny brown flecks in a position comparable to that of the fully developed seed (Pl. III, Fig. 3). In the McIntosh, the ovules, generally ten or more as in the Wagener, fail to orient themselves in a position close to the locular wall. The ovule itself in its young stage swings through an angle of 90° to become anatropous, but the angle is, in general, a horizontal one, not vertical as in Wagener. In some cases the ovules are extended so that they may even reach the opposite wall of the locule ; in others they are pushed into the central cavity at the axis (Pl. II, Fig. 3). Thus the cavity may simulate an ovary in the McIntosh. A transverse section of the carpellary region of McIntosh (Pl. II, Fig. 3) shows ovules in longitudinal section owing to their orientation in the locules. A transverse section through a similar region of Wagener shows the ovules in cross section (Pl. II, Fig. 4). These two figures typify the difference in orientation of the ovules in the two varieties.

Locules in both varieties are bi-partite. This partial division is brought about by a protuberance or lamina extending into the locule opposite the dorsal carpel bundle (Pl. II, Figs. 3, 4). As Bonne (1, page 217) has noted for *Pyrus communis,* the protuberance becomes more marked at the summit of the locule. This projection at the apex is much more marked in Wagener than in McIntosh. In Wagener it completely divides the apex of the locule into two parts.

DISCUSSION.

A comparison of the primary vascular patterns in the two varieties indicates differences in the levels at which the staminal bundles originate. The circles of stamens are attached to the basin at a lower level in the McIntosh than in the Wagener. The cortical reticulum is more extensive and coarser in McIntosh. When the carpellary systems are compared, the most striking differences are: (1) the outlines of the carpellary network ; widely divergent at the sides of the locules and dorsally truncated in Wagener, closely following the sides and dorsally pointed in McIntosh ; (2) a correspondingly greater width of tissue between this network and the carpellary network in Wagener ; and (3) the regularity of orientation of ovules coincident with regularity in the separation of the ovular traces from the ventral bundles in Wagener, while in McIntosh irregularity of orientation of the ovules coexists with irregularity in the separation and direction of the ovular traces.

In Wagener, centripetal growth of the ventral lobes, in addition to increasing the radial diameter of the locules, brings the ventral lobes of the carpels close to

the axis. This, accompanied by the infolding of the margins in the formation of the placentae, causes the formation of the " closed " core. The locules are not open to the central cavity. In contrast, tangential growth in the carpellary region, relatively greater than the centripetal growth of the ventral lobes, as seems to occur in McIntosh, would cause (1) failure of the ventral lobes to approach the axis, and (2) failure of " fusion " of the margins of the ventral lobes. The former tends to produce a large central cavity ; and the latter leaves the locules open to the central cavity. This is the " open " core of McIntosh (Pl. III, Fig. 2* and Pl. II, Fig. 3). Again, should growth in the ovules of McIntosh be greater than that of the surrounding tissue, in the early stages at least, a further cause for the phenomenon of " open " core and the peculiar orientation of the ovules would be demonstrated. Moreover, in the later stages, the greater depth of basin and cavity in Wagener is apparently due to a comparatively greater upward and radial direction of growth of the cortical cells at the apex, and a corresponding downward and radial growth of the cortical cells at the base.

The origin of " open " core begins early in ontogeny. At first both varieties are definitely " open-cored " (Pl. II, Fig. 2). The internal cavity in the young bud is cup-shaped. During subsequent development this hollow structure becomes gradually closed over from the margin. Growth in the carpellary region, a growth which is directed from the periphery towards the centre and from the base towards the summit, " closes " the core of Wagener leaving only the central cavity (Pl. II, Fig. 4 and Pl. III, Fig 1†). The carpel tissue in the early stages may, by its staining reaction, be distinguished from the outer tissues. It can be seen (Pl. II, Fig. 2) that the carpels lining the cup are joined by their dorsal faces to these outer tissues. This could be interpreted as histological evidence of (1) toral tissue supporting sporogenous tissue, or (2) the phylogenetic adnation of the carpels to the tissues of the outer whorls. If the latter, the current interpretation, be accepted, then " fusion " of organs is evident, and it is to be expected that a certain amount of " fusion " occurs in the skeletal tissues. Such " fusion " is found between the staminal and the perianth bundles. Although the outer whorls are " fused " with the ovary, the skeletal tissue of the carpels remains distinct from that of the periantho-staminal skeletal tissue, from the point of origin of the former at the apex of the pedicel. The conditions are very similar to those in Gaylussacia (Eames (2)), with the single exception that no " fusion " whatsoever occurs between the dorsal carpel bundles and the united sepal-stamen bundle in these two varieties

* The " open " core of McIntosh is accentuated in this figure, due to shrinkage during the clearing process.

† During the clearing process a certain amount of shrinkage occurs. This accounts for the two " open " locules in the figure.

of the apple. For this reason these two varieties of apple would serve as even better examples of the "fusion" of the outer whorls with the carpels than Gaylussacia, but having the skeletal tissue of the outer whorls distinct. The periantho-staminal vascularization (Pl. I, Fig. 5) is somewhat similar to that of *Crossosoma Bigelovii* Wats. (Wilson (15)). In McIntosh Red and Wagener there is no exception to the "fusion" of stamen traces with either the sepal or the petal bundle. Sepal and petal bundles are entirely separate from each other, and these petal bundles, as in the separate petal bundles of *C. Bigelovii*, give off laterals to the sepals.

The five ovaries of each of these two varieties of apple are more or less bilocular. Saunders (11, p. 610), in discussing *Amelanchier canadensis* Torr. and Gray, says: "This genus is unique almost among the Rosaceae in having more or less bilocular ovaries", and in a footnote mentions that "The only other case, apparently, is that of Parinarium." Her figures 178 and 179 of *A. canadensis* show the condition of bi-partite loculi identical with that of McIntosh Red (Pl. II, Fig. 3) and Wagener (Pl. II, Fig. 4) in the present paper. Her explanation of the origin of the bilocular condition is that the laminae are the sterile carpels of a polymorphic carpel system, and that there is an incomplete withdrawal of this sterile carpel from the central column of tissue at the axis of the fruit. However, in these two varieties of apple, there is no central column of tissue; a central cavity occupies the axial region. An examination of Pl. II, Figs. 2, 3 and 4 shows that the carpels achieve their ultimate form by an active period of centripetal marginal growth, although this is in direct contradiction to Saunder's (10) explanation of the formation of carpels.

Observation of the skeletal tissue discloses that the dorsal bundles are the last branches given off by the anticlinal division or dichotomy of the primary vascular strands. Immediately above this point the primaries diverge, and the carpellary bundles pass up into the carpels. Further divisions of the primary bundles, giving rise to (1) secondaries ramifying into the cortex and (2) the staminal bundles, are all periclinal or tangential. Since no gaps are left, the writers are inclined to the view that the receptacle of the apple ends at the point of departure of the dorsal carpel traces (Pl. I, Fig. 3a). In their judgment the fleshy part of the apple is essentially a calyx-tube; that is, the consolidated bases of the members of the calyx, corolla and stamens. This accords with Eames' and MacDaniels' interpretation (3). A much more descriptive term than "calyx-tube" is Bonne's "floral cup".

If the vascular system of an organ be accepted as significant from a comparative morphological point of view, then the present study offers no support to the thesis of J. McL. Thompson (14). If anatomical evidence be discarded as significant in interpreting floral morphology, the present study, as

early pointed out (page 229), could be supportive. It also seems difficult to find support for the interpretation of the fleshy part of the apple pome—as exemplified by the two varieties studied—as receptacular.

SUMMARY.

1. A comparative study of the vascular anatomy of the fruits of two apple varieties, McIntosh Red and Wagener, shows that the outline of the primary vascular bundles in McIntosh Red approaches that of a circle, while in Wagener a lobed outline, giving the appearance of an inner and an outer circle, is evident. This is concurrent with the definite angulation of the Wagener fruit.

2. The cortical reticulum of McIntosh is denser than that of Wagener. Secondary branches from the periantho-staminal complex are seldom paired. Anastomoses between them are more frequent. Staminal bundles arise from the periantho-staminal complex at a lower point in McIntosh than in Wagener, and also enter the filaments at a lower point on the side of the basin.

3. The line of division between pith and cortex is very irregular in McIntosh, but shows a definite regular pattern in Wagener. The external carpellary network of McIntosh closely follows the endocarp. It is more distant from the endocarp in Wagener, is truncated in the region of the dorsal carpel bundle, and shows more fleshy tissue between the network and the endocarp.

4. The ovules of Wagener are longitudinally oriented in the bi-partite locules, one ovule in each half of the locule. There is no such regularity of ovule orientation in McIntosh. They are generally horizontal in position, stretching across the bi-partite locule or occupying the central cavity at the axis. The paired ventral bundles are often united by their phloem faces.

5. The core of McIntosh is "open"; that is, the ventral lobes of the carpels during development never completely unite, so that the locules are never completely separated from the central cavity. The core of Wagener is developmentally "closed". The central cavity is small. The ventral lobes of a carpel "fuse", and thus no opening connects the locule with the central cavity.

6. There is no evidence of carpel polymorphism. The ovary is regularly composed of five carpels.

7. In accord with the evidence presented, the writers are inclined to view the fleshy part of the fruit external to the core line as a fleshy *floral cup*.

The writers are grateful to Dr. W. S. Blair, Superintendent of the Dominion Experimental Farm, Kentville, Nova Scotia, for placing at their disposal the fruit trees selected for the experiment and to Mr. C. C. Eidt for his assistance and advice during the field work.

LITERATURE REFERENCES.

(1) *Bonne, G.* Recherches sur le pedicelle et la fleur des Rosacées. Doctor's Thesis, 1928, Paris, 377 pp.

(2) *Eames, A. J.* The vascular anatomy of the flower with refutation of the theory of carpel polymorphism. Amer. Journ. Bot., 1931, **18**, 147.

(3) ——— and *MacDaniels, L. H.* Introduction to plant anatomy. 1925. McGraw-Hill Book Co., New York.

(4) *Grew, N.* The Anatomy of Plants. 1682, 2nd edition. London.

(5) *Hall, A. D.* and *Crane, M. B.* The apple. 1933. Martin Hopkinson Ltd., London.

(6) *Hunt, K. W.* A study of the style and stigma, with reference to the nature of the carpel. Amer. Journ. Bot., 1937, **24**, 288.

(7) *Kraus, E. J.* The pollination of the pomaceous fruits. I. Gross morphology of the apple. Oreg. Agric. Coll. Expt. Sta. Res. Bull. No. 1, 1913.

(8) ———. Variation of the internal structure of apple varieties. Oreg. Agric. Coll. Expt. Sta., 1916, Sta. Bull. No. 135.

(9) ——— and *Ralston, G. S.* The pollination of the pomaceous fruits. III. Gross vascular anatomy of the apple. Oreg. Agric. Coll. Expt. Sta., 1916, Sta. Bull. No. 138.

(10) *Saunders, E. R.* On carpel polymorphism. I. Ann. Bot., 1925, **39**, 123.

(11) ———. On carpel polymorphism. II. Ann. Bot., 1927, **41**, 569.

(12) *Tetley, U.* A study of the anatomical development of the apple and some observations on the "pectic constituents" of the cell-walls. Journ. Pom. & Hort. Sci., 1930, **8**, 153.

(13) ———. The morphology and cytology of the apple fruit, with special reference to Bramley's Seedling variety. Journ. Pom. & Hort. Sci., 1931, **9**, 278.

(14) *Thompson, J. McL.* Studies in advancing sterility. VII. The state of flowering known as angiospermy. Pub. Hartley Bot. Lab., 1934, No. 12.

(15) *Wilson, C. L.* The phylogeny of the stamen. Amer. Journ. Bot., 1937, **24**, 686.

(16) *Zirkle, C.* The use of n-butyl alcohol in dehydrating woody tissue for paraffin method. Sci., 1930, **71**, 103.

(*Received* 12/3/39.)

PLATE II.

1

2

3

4

FIG. 1. Transverse section of pedicel of the apple showing traces to bracts. (×40.)

FIG. 2. Median transverse section through bud of apple showing initiation of ventral carpel lobes and carpel tissue lining the "cup". (×40.)

FIG. 3. Median transverse section of McIntosh Red showing irregular orientation of ovules. (×27.)

FIG. 4. Median transverse section of Wagener showing regular orientation of ovules. (×13.)

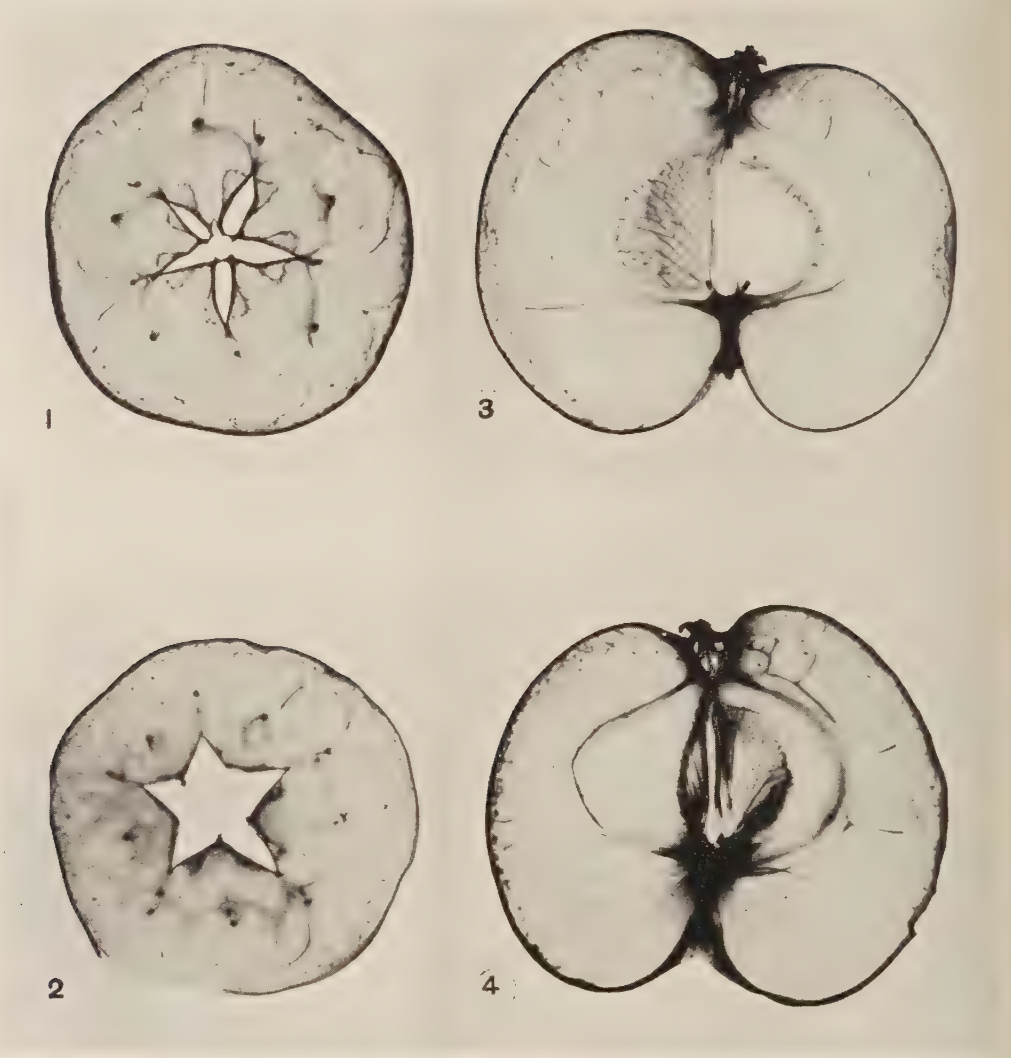


FIG. 1. Median transverse cleared section of Wagener showing " closed " core, lobed outline of tissue marking line of division between cortex and carpel tissue, carpellary network distant from locule, paired secondary branches, and peripheral vascular network. (Two locules " open " owing to shrinkage in clearing.)

FIG. 2. Median transverse cleared section of McIntosh Red showing " open " core, angular outline of tissue between cortex and carpel tissue, carpellary network close to locules, and single secondary branches.

FIG. 3. Median longitudinal cleared section of Wagener showing position of stamens in basin, aborted ovules, direction of secondary branching, peripheral vascular network and carpellary network.

FIG. 4. Median longitudinal cleared section of McIntosh Red showing position of stamens in basin, direction of secondary branching, peripheral vascular network and carpellary network.

SEASONAL VARIATIONS OF STARCH CONTENT IN THE GENUS ROSA, AND THEIR RELATION TO PROPAGATION BY STEM CUTTINGS

By DOROTHY BRANDON
Department of Horticulture, University of Reading

Roses have been cultivated for many centuries and have been the subject of more intensive breeding than any other ornamental plant. Yet, apart from this breeding work (which has largely been haphazard and unscientific), rose material has rarely been chosen as a subject of scientific investigation. Very few experiments on vegetative propagation by stem cuttings have included roses, yet such cuttings provide an interesting problem, in that some are easy to root (e.g. the common stocks and the hybrid *multifloras*), and others are extremely difficult (e.g. *R. foetida, R. Hugonis, R. Willmottiae* and *R. Moyesii*). This difficulty of rooting rose stem cuttings is one of the chief reasons for the practice of propagating this plant by budding and grafting. The studies on rose stocks of such workers as Ferguson (8) and Yerkes (18) have put the practice on a more scientific basis by the classification of the stocks botanically, and by some investigation of the influence of stock on scion. In view of the small amount of information available on the relative ease of rooting of different members of the genus, a series of experiments was designed to study these differences, and also to determine the effect of certain methods of treatment which might encourage rooting.

It has been suggested by Carlson (2) that a high starch content is correlated with easy rooting. A series of microscopic examinations was therefore included in the studies, in order to investigate this point in greater detail, and this produced interesting information on the starch fluctuations during the season. Seasonal starch variations have been followed in the apple by Smyth (13, 14), Kraybill, Sullivan and Miller (12), Swarbrick (15), and a few other workers. The fluctuations in Rosa are compared in this paper with the findings of these investigators. From its beginning as an incidental phenomenon in relation to the rooting of cuttings, the present investigation was expanded into an observation of the seasonal fluctuations in starch content of a large number of species and varieties of the genus Rosa, and this work is included in the present paper for its independent value.

Methods.

Preparation of Cuttings and Handling Subsequent to Treatment.

The findings of various workers with other genera were considered in planning the experiments. Thus, when making the cuttings, the work of Esper

and Roof (7), and Calma and Richey (1), which showed that reduction of foliage decreased rooting, was taken into account. Hitchcock and Zimmerman (9) concluded that, in most instances, "heel" and "mallet" cuttings failed to root so well as cuttings made at a node, although the method was beneficial in a few cases, including one species of Rosa. Chadwick (3, 4) showed that a basal cut below the node is preferable with most plants to one at or above the node.

In a preliminary trial, the following species and varieties were selected from the material available at the University Horticultural Station:—

1.	*Rosa canina* L.	Dog Rose.
2.	,, ,,	Kokulensky's Strain.
3.	,, ,,	Senff's Strain.
4.	,, *centifolia muscosa* Ser.	Moss Rose.
5.	,, *coriifolia Froebelii* Rehd.	*Laxa* Stock.
6.	,, Hybrid *bracteata*	Mermaid.
7.	,, ,, *multiflora*	De la Grifferaie.
8.	,, ,, ,,	Philadelphia Rambler.
9.	,, ,, Perpetual	Frau Karl Druschki.
10.	,, ,, ,,	Mrs. John Laing.
11.	,, ,, Tea	Climbing Ophelia.
12.	,, ,, ,,	Mrs. Oakley Fisher. (Heel and node cuttings.)
13.	,, ,, *Wichuraiana*	Chaplin's Pink.
14.	,, *foetida* Herrm.	(Syn. *R. lutea* Mill.). Austrian Briar. (Heel, node and internode cuttings.)
15.	,, *Manetti* Crivelli	*Manetti* Stock.
16.	,, ,, *Lippiat* Hort.	
17.	,, *moschata floribunda* Hort.	(Node and internode cuttings.)
18.	,, *multiflora* Thunb.	Variety unidentified.
19.	,, ,,	Seabrook's *polyantha* Stock.
20.	,, "*odorata*"	(Stock of obscure origin. Not *R. odorata* Sweet.) (Node and internode cuttings.)
21.	,, *rubiginosa* L.	Sweet Briar.
22.	,, *rugosa* Thunb.	Japanese Rose.
23.	,, ,, *rubra* Hort.	Rose Apple, Hedgehog Rose.
24.	,, ,, × *canina*	Smit's Briar.
25.	,, "*setigera*" Hort.	(Stock of obscure origin. Not *R. setigera* Michx.)
26.	,, *Willmottiae* Hemsl.	(Heel and node cuttings.)

The cuttings were nodal unless otherwise stated, the cut being clean and horizontal, ⅛ in. below the node. The diameter at the point of severance was 0·8-1·0 cm. for *R. moschata floribunda* and Hybrid *Wichuraiana*, 0·6-0·8 cm. for *R. canina*, *R. multiflora* and *R. Willmottiae* (nodal cuttings), and approximately 0·3 cm. above the heel for *R. Willmottiae* (heel cuttings). In some cases it was possible to make heel and internode cuttings also; these are indicated in the foregoing list. Fifty cuttings of each were made, divided into five samples of ten, for different treatments. The first experiment was a trial with small samples of a large number of varieties, to obtain some indication of the relative rooting capacities and response to treatments. According to the performance of these, and also depending on the material available, a smaller number was afterwards selected for work with larger samples, these being:—

1.	*Rosa canina*	Senff's Strain.
2.	,, ,,	Kokulensky's Strain.
3.	,, *moschata floribunda*	
4.	,, *multiflora*	Seabrook's *polyantha* Stock.
5.	,, *Willmottiae*	
6.	,, Hybrid *multiflora*	Kirsten Poulsen. (In later trials only.)
7.	,, ,, *Wichuraiana*	Paul's Scarlet. (This replaced Chaplin's Pink in the previous list.)

The nodal and internodal cuttings were about eight, and the heel cuttings about five inches long. When present, the leaves were reduced a little to make handling easier and to give approximately the same leaf area to each cutting. After treatment, hardwood cuttings were lined out in the open ground three inches apart in rows one foot apart, and softwood cuttings were inserted in silver sand in galvanized iron propagating trays at about 60° F.

TREATMENTS.

(a) *Variation of Time of Insertion.*

Late autumn is the usual time for taking hardwood cuttings of roses, but batches were inserted in October, December and January to ascertain the effect of season on rooting. Softwood cuttings were taken in June and July. The dates were as follows:—

Batch I.	October 25th, 1935.
,, II.	October 6th-9th, 1936.
,, III.	December 1st-6th, 1936.
,, IV.	January 11th, 1937.
,, V.	June 3rd, 1937.
,, VI.	July 3rd, 1937.

(b) *Variation of Chemical Treatments.*

Certain chemical compounds have been shown to be effective in breaking the dormancy of buds in woody plants (Denny (5), Denny and Stanton (6)), and it was decided to try two of these as rooting accelerators, namely ethylene chlorhydrin and thiourea. The latter was used in solution, and the ethylene chlorhydrin both in solution and as a vapour. Sodium nitrate has also been used as a dormancy breaker, though without pronounced effect, and this also was included in the treatments. Glucose has been shown to stimulate the rooting of some cuttings (Klein (11)), and it was used in these trials in two concentrations. The synthetic growth hormone β-indolyl-acetic-acid, well known as an effective agent in the initiation of roots (Hitchcock and Zimmerman (10), Tincker (16), and subsequent workers), was included in the second year of the trials. The treatments, therefore, were as follows:—

A	Ethylene chlorhydrin	1·5% solution.
A_1	,, ,,	2 cc. per litre, vapour.
B	Thiourea	1% solution.
C	Sodium nitrate	0·5% ,,
D	Glucose	1% ,,
D_1	,,	5% ,,
E	β-indolyl-acetic-acid	1 in 10,000 solution.
E_1	,,	1 ,, 25,000 ,,
E_2	,,	1 ,, 50,000 ,,
F	Tap water Control.	

The cuttings were placed with their bases in 2-3 inches of solution for twenty-four hours and then rinsed. In the treatment with ethylene chlorhydrin vapour, they were placed in an air-tight box of known capacity for three days, together with the necessary quantity of ethylene chlorhydrin on cotton wool.

(c) *Variation of pH of Solution.*

The last batch of softwood cuttings (Batch VI in July 1937) was also employed for an investigation of the effect of the pH of the solution (β-indolyl-acetic-acid or water) on the rooting of the cuttings. Two pH values, 5 and 7, and β-indolyl-acetic-acid and water gave four possible combinations, and these were tried in triplicate.

RESULTS OF ROOTING TRIALS.

The results obtained are given in Tables I and II, in which the numbers of cuttings showing any roots are given in the second column for each treatment. Large differences in the number of roots produced were found, and in many cases the cuttings that had not rooted had callused. Nevertheless, the numbers given provide at least some indication of the relative ease of rooting of the different types, and further details would greatly complicate the issue without providing much additional information.

TABLE I.

Results with Hardwood Cuttings.

(x = number inserted, y = number rooted.)

Date.	Species.	Treatments.																			
		A		A_1		B		C		D		D_1		E		E_1		E_2		F	
		x	y	x	y	x	y	x	y	x	y	x	y	x	y	x	y	x	y	x	y
I (Oct.)	*canina*	—	—	—	—	—	—	10	5	10	9	—	—	—	—	—	—	—	—	10	1
	,, Kokulensky's ..	10	8	—	—	10	10	10	10	10	10	—	—	—	—	—	—	—	—	10	10
	,, Senff's	—	—	10	—	10	8	10	9	10	8	—	—	—	—	—	—	—	—	10	—
	centifolia muscosa	—	—	10	—	10	10	10	10	10	8	—	—	—	—	—	—	—	—	10	10
	coriifolia Froebelii	—	—	10	—	10	10	10	10	10	3	—	—	—	—	—	—	—	—	10	1
	H. *bracteata* Mermaid ..	—	—	10	—	10	—	10	—	—	—	—	—	—	—	—	—	—	—	10	—
	H. *multiflora* De la Grifferaie	—	—	10	—	10	—	10	10	10	10	—	—	—	—	—	—	—	—	10	10
	,, Phil. Rambler ..	10	10	—	—	10	2	—	—	—	—	—	—	—	—	—	—	—	—	10	9
	H.P. Frau Karl Druschki ..	10	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	—
	H.T. Climbing Ophelia ..	10	7	—	—	10	2	10	—	—	—	—	—	—	—	—	—	—	—	10	10
	H.T. Mrs. Oakley Fisher ..	—	—	—	—	10	—	10	—	10	—	—	—	—	—	—	—	—	—	10	—
	,, (heel)	—	—	10	—	10	—	10	—	10	—	—	—	—	—	—	—	—	—	10	—
	H. *Wich.* Chaplin's Pink ..	10	4	10	—	10	9	10	6	10	9	—	—	—	—	—	—	—	—	10	10
	foetida	10	9	—	—	10	6	10	1	10	1	—	—	—	—	—	—	—	—	10	6
	,, (heel)	10	10	—	—	10	—	10	10	10	5	—	—	—	—	—	—	—	—	10	9
	,, (internode)	10	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	10	6
	Manetti	10	10	—	—	10	9	10	10	10	9	—	—	—	—	—	—	—	—	10	1
	,, *Lippiat*	10	9	—	—	10	10	10	10	10	—	—	—	—	—	—	—	—	—	10	4
	moschata floribunda	10	3	—	—	10	—	10	9	10	6	—	—	—	—	—	—	—	—	10	4
	,, (internode)	10	3	—	—	10	1	10	5	10	2	—	—	—	—	—	—	—	—	10	2
	multiflora, unidentified ..	—	—	10	—	10	—	10	10	10	10	—	—	—	—	—	—	—	—	10	10
	,, Seabrook's ..	—	—	—	—	10	3	10	8	10	8	—	—	—	—	—	—	—	—	10	4
	"*odorata*"	10	9	—	—	10	8	10	7	10	9	—	—	—	—	—	—	—	—	10	10
	,, (internode)	—	—	—	—	—	—	10	10	10	10	—	—	—	—	—	—	—	—	10	10
	rubiginosa	—	—	10	—	10	—	10	—	10	—	—	—	—	—	—	—	—	—	10	—
	rugosa	—	—	10	—	10	10	10	10	10	10	—	—	—	—	—	—	—	—	10	10
	,, *rubra*	—	—	10	10	10	10	10	10	10	10	—	—	—	—	—	—	—	—	10	10
	,, × *canina,* Smit's ..	10	10	—	—	10	10	10	9	10	10	—	—	—	—	—	—	—	—	10	10
	"*setigera*"	10	10	—	—	10	9	10	10	10	10	—	—	—	—	—	—	—	—	10	10
	Willmottiae	—	—	10	—	10	—	10	—	10	—	—	—	—	—	—	—	—	—	10	—
	,, (heel)	—	—	10	—	10	—	10	—	10	—	—	—	—	—	—	—	—	—	10	—
II (Oct.)	*canina* Senff's	—	—	—	—	—	—	—	—	50	8	50	8	—	—	—	—	—	—	50	5
	moschata floribunda	—	—	—	—	—	—	—	—	50	47	—	—	—	—	—	—	—	—	50	40
	multiflora Seabrook's ..	—	—	—	—	—	—	—	—	50	39	50	43	—	—	—	—	—	—	50	34
	Willmottiae	—	—	—	—	—	—	—	—	50	—	50	—	—	—	—	—	—	—	50	—
	,, (heel)	—	—	—	—	—	—	—	—	50	—	—	—	—	—	—	—	—	—	50	—
	Paul's Scarlet Climber ..	—	—	—	—	—	—	—	—	50	3	50	9	—	—	—	—	—	—	50	4
	Kirsten Poulsen	—	—	—	—	—	—	—	—	50	4	50	6	—	—	—	—	—	—	50	12
III (Dec.)	*canina* Senff's	—	—	—	—	—	—	—	—	—	—	—	—	50	27	—	—	—	—	50	29
	moschata floribunda	—	—	—	—	—	—	—	—	—	—	50	13	50	8	—	—	50	8	50	42
	multiflora Seabrook's ..	—	—	—	—	—	—	—	—	50	16	50	30	—	—	—	—	50	32	50	9
	Willmottiae	—	—	—	—	—	—	—	—	50	—	50	—	50	—	—	—	50	—	50	—
	,, (heel)	—	—	—	—	—	—	—	—	50	—	50	—	50	—	—	—	50	—	50	—
	Paul's Scarlet Climber ..	—	—	—	—	—	—	—	—	50	9	—	—	50	12	—	—	—	—	50	13
	Kirsten Poulsen	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	17	50	—
IV (Jan.)	*canina* Senff's	—	—	—	—	—	—	—	—	—	—	—	—	—	—	45	8	—	—	45	13
	multiflora Seabrook's ..	—	—	—	—	—	—	—	—	40	36	50	—	—	—	50	37	—	—	50	29
	Willmottiae	—	—	—	—	—	—	—	—	40	—	—	—	—	—	40	—	—	—	40	—
	,, (heel)	—	—	—	—	—	—	—	—	50	—	50	—	—	—	50	—	—	—	50	—
	Paul's Scarlet Climber ..	—	—	—	—	—	—	—	—	40	11	40	1	—	—	40	10	—	—	40	5

TABLE II.

Results with Softwood Cuttings

(x = number inserted, y = number rooted.)

Date.	Species.		Treatments. D x	D y	E x	E y	E_1 x	E_1 y	E_2 x	E_2 y	F x	F y
V (June)	*R. canina* Senff's	1	15	—	15	—	—	—	15	—	15	—
		2	15	—	15	—	—	—	15	1	15	—
		3	15	—	15	2	—	—	15	—	15	4
	R. multiflora Seabrook's ..	1	15	10	15	4	—	—	15	12	15	10
		2	15	7	15	9	—	—	15	7	15	10
		3	15	14	15	7	—	—	15	11	15	10
VI (July)	*R. multiflora* Unidentified											
	pH 5	1	—	—	—	—	30	23	—	—	30	21
	,,	2	—	—	—	—	30	17	—	—	30	22
	,,	3	—	—	—	—	30	17	—	—	30	21
	pH 7	1	—	—	—	—	30	25	—	—	30	19
	,,	2	—	—	—	—	30	23	—	—	30	17
	,,	3	—	—	—	—	30	23	—	—	30	18

Discussion of Results.

(1) *Effect of Variety.*

As will be seen from Table I, variety is the chief factor influencing the rooting of rose cuttings. Certain varieties did not root under any conditions. Among these were:—

Rosa bracteata	Mermaid.
,, *foetida*	(Heel, node and internode cuttings.)
,, H.P.	Frau Karl Druschki.
,, H.T.	Mrs. Oakley Fisher.
,, *rubiginosa.*	
,, *Willmottiae*	(Heel and node cuttings.)

Others rooted well under most conditions, such as:—

Rosa multiflora	De la Grifferaie.
,, ,,	Philadelphia Rambler.
,, ,,	Seabrook's.
,, ,,	Unidentified.
,, "*odorata*".	
,, *rugosa.*	
,, ,, *rubra.*	
,, ,, × *canina*	Smit's Briar.
,, "*setigera*".	

It is significant that all the *R. rugosa* varieties and all the *R. multiflora* varieties fall into one group, indicating that rooting capacity is an inherent phenomenon in a species. Varietal susceptibility to certain reagents is also noticeable. In the thiourea treatment, all the *rugosa* varieties responded well, each rooting 100%, whereas all the *multiflora* varieties gave low figures.

In Batch V, although prepared in triplicate, there was no close agreement between replicates, even though every precaution was taken to ensure uniform material and conditions. Such variation shows that large numbers of cuttings must be used to give significant results, otherwise the effect of treatment is masked. Batches II, III and IV, with fifty cuttings each, were adequate, but the lot of fifteen in Batch V was insufficient.

(2) *Effect of Time of Insertion.*

In Table III, percentage figures are given, for ease of comparison. Batches II and III gave very similar results and showed considerably higher figures than Batch IV, indicating that October to December is a better time than January for taking hardwood cuttings. This substantiates the findings of horticultural practice. The softwood cuttings of June and July showed a very good response for *R. multiflora,* but *R. canina* did not give such a good percentage as when taken in the winter.

TABLE III.

Percentage Rooting.

Species.	Date of Insertion.									
	II. (Oct.)		III. (Dec.)		IV. (Jan.)		V. (June)		VI. (July)	
	% of Total.	% of Untreated.	% of Total.	% of Untreated.	% of Total.	% of Untreated.	% of Total.	% of Untreated.	% of Total.	% of Untreated.
R. canina Senff's	15	10	56	58	23	29	3	9	—	—
R. moschata floribunda	87	80	36	84	—	—	—	—	—	—
R. multiflora Seabrook's	77	68	44	18	54	58	62	67	71	70
R. Willmottia	0	0	0	0	0	0	—	—	—	—
,, (heel cuttings)	0	0	0	0	0	0	—	—	—	—
Paul's Scarlet Climber	11	8	23	26	17	13	—	—	—	—
Kirsten Poulsen	14	20	28	0	—	—	—	—	—	—
Mean	29	27	27	27	19	20	33	38	71	70

(3) *Effect of Chemical Treatments.*

From Table I it will be seen that 1% glucose had a slightly beneficial effect on the rooting of every batch. The results with 5% glucose were variable, but showed in most cases a disadvantageous effect. Sodium nitrate was used only in Batch I, where the numbers are too small for significance ; but there is an indication of a beneficial effect. Ethylene chlorhydrin in 1·5% solution had no apparent effect, but was exceedingly toxic as a vapour, *R. rugosa rubra* alone surviving the treatment. The resistance of this species to the vapour may lie in the great thickness of its cortex, which may protect the underlying tissues. Thiourea also exerted a harmful effect, though certain species tended to resist it. β-indolyl-acetic-acid was unfortunately unobtainable until Batch III was started. It did not give so great an increase in the rooting of rose cuttings as it has been shown to do with other woody subjects (Hitchcock and Zimmerman (10), Tincker (16, 17)), but it is likely that the optimum concentration or the best method was not employed. A concentration of 1 in 10,000 appeared to be too high, but a slight improvement in rooting was obtained with the lower concentrations.

(4) *Effect of pH of Solution.*

The pH value of the solution appears to have little effect on the subsequent rooting of the cuttings. With β-indolyl-acetic-acid those at pH 7 rooted best, but with water, those at pH 5 showed a higher percentage of rooting. Subsequent work on the effect of the pure silica sand on the reaction of such slightly buffered solutions as those used indicate that the pH of the solutions was unlikely to remain constant for a long period after their application to the sand.

SEASONAL STARCH FLUCTUATIONS.

It has been shown by Carlson (2) that closely allied varieties of the genus Rosa may show a dissimilarity in the starch content of their stems, but the varieties under investigation were only two in number—Dorothy Perkins and American Pillar, both Hybrid *Wichuraianas*. As mentioned above, a more extensive investigation was carried out in the present work, in which a large number of species and varieties were used. Most of the varieties used in the experiments on propagation were studied, together with others which were of possible interest, as follows :—

1.	*Rosa arvensis* Huds.	Field Rose.
2.	,, *canina* L.	Dog Rose.
3.	,, ,,	Brog's Strain.
4.	,, ,,	Deegan's Strain.
5.	,, ,,	Jägerbataillon Strain.
6.	,, ,,	Kokulensky's Strain.

7.	*Rosa canina* L.	Senff's Strain.
8.	,, ,,	Schmidt's Ideal Strain.
9.	,, ,,	Weidensweiler Strain.
10.	,, *centifolia muscosa* Ser.	Moss Rose.
11.	,, *coriifolia Froebelii* Rehd.	(Syn. *R. laxa* Froed.) *Laxa* Stock.
12.	,, *damascena* Mill.	Crimson Damask.
13.	,, *foetida* Herrm.	(Syn. *R. lutea.* Mill.) Austrian Briar.
14.	,, *Hugonis* Hemsl.	
15.	,, Hybrid *bracteata*	Mermaid.
16.	,, ,, *multiflora*	De la Grifferaie.
17.	,, ,, Musk	Penelope.
18.	,, ,, Perpetual	Hugh Dickson.
19.	,, ,, Tea	Betty Uprichard.
20.	,, ,, ,,	Climbing Lady Waterlow.
21.	,, ,, ,,	Madame Butterfly.
22.	,, ,, *Wichuraiana*	Paul's Scarlet Climber.
23.	,, ,, ,,	René André.
24.	,, ,, *multiflora*	(Syn. *R. polyantha* Hort.) Kirsten Poulsen.
25.	,, ,, ,,	Yvonne Rabier.
26.	,, *Manetti* Crivelli.	*Manetti* Stock.
27.	,, ,, var. *Lippiat* Hort.	
28.	,, *moschata floribunda* Hort.	
29.	,, *Moyesii* Hemsl. and Wils.	
30.	,, ,, var. *Fargesii* Rolfe.	
31.	,, *multiflora* Thunb.	
32.	,, "*odorata*"	(Stock of obscure origin. Not *R. odorata* Sweet.)
33.	,, *omeiensis* var. *pteracantha* Rehd. and Wils.	(Syn. *R. sericea* var. *pteracantha* Fr.)
34.	,, *pomifera* Herrm.	Apple Rose.
35.	,, *rubiginosa* L.	Sweet Briar.
36.	,, *rubrifolia* Vill.	
37.	,, *rugosa* Thunb.	Japanese Rose.
38.	,, ,, var. *rubra* Hort.	Hedgehog Rose, Rose Apple.
39.	,, ,, × *canina*	Smit's Briar.
40.	,, "*setigera*"	(Stock of obscure origin. Not *R. setigera* Michx.)
41.	,, *spinosissima* L.	Burnet Rose.
42.	,, *Willmottiae* Hemsl.	

Microscopical investigation of the stems of the above varieties was carried out at the beginning of every month from November to July inclusive. Healthy, first-year wood was selected and preserved immediately in 80% alcohol. The sections were cut midway between two nodes, using a Jung sliding microtome with a special holder for non-embedded hardwood. They were stained with KI-iodine, mounted in glycerine, and the distribution of starch in the following tissues was recorded: (1) Small cells of pith ; (2) Outer pith ; (3) Primary medullary rays ; (4) Secondary medullary rays ; (5) Xylem parenchyma ; (6) Phloem rays ; (7) Phloem parenchyma ; (8) Sclerenchyma ; (9) Inner cortex ; (10) Outer cortex ; (11) Subepidermis ; (12) Epidermis.

RESULTS OF STARCH INVESTIGATION.

Starch fluctuations typical of all perennial stems were observed. Starch had accumulated by the end of autumn, and this reserve showed a gradual depletion during the winter months. Throughout the period the medullary ray tissue maintained the highest starch content and was the last to lose its starch in the winter. The outer pith also ranked high in starch content. The sclerenchyma and epidermis never contained starch, except the guard cells of the stomata of the latter. The small cells of the pith were never packed with starch, and they tended to lose what they contained early in the winter. Very occasionally a few grains were observed in the xylem parenchyma but starch was more frequent in the phloem rays and parenchyma. Both outer and inner cortex showed a moderate quantity, and the inner cortex became depleted first.

The varieties with little starch were usually entirely depleted early in the season (e.g. *R. Moyesii Fargesii*), and those with abundant starch in the beginning retained a little throughout (e.g. *R. canina*). In some cases hardly any was lost (e.g. *R. multiflora* De la Grifferaie). These general results were to be expected, but the minor differences are of interest.

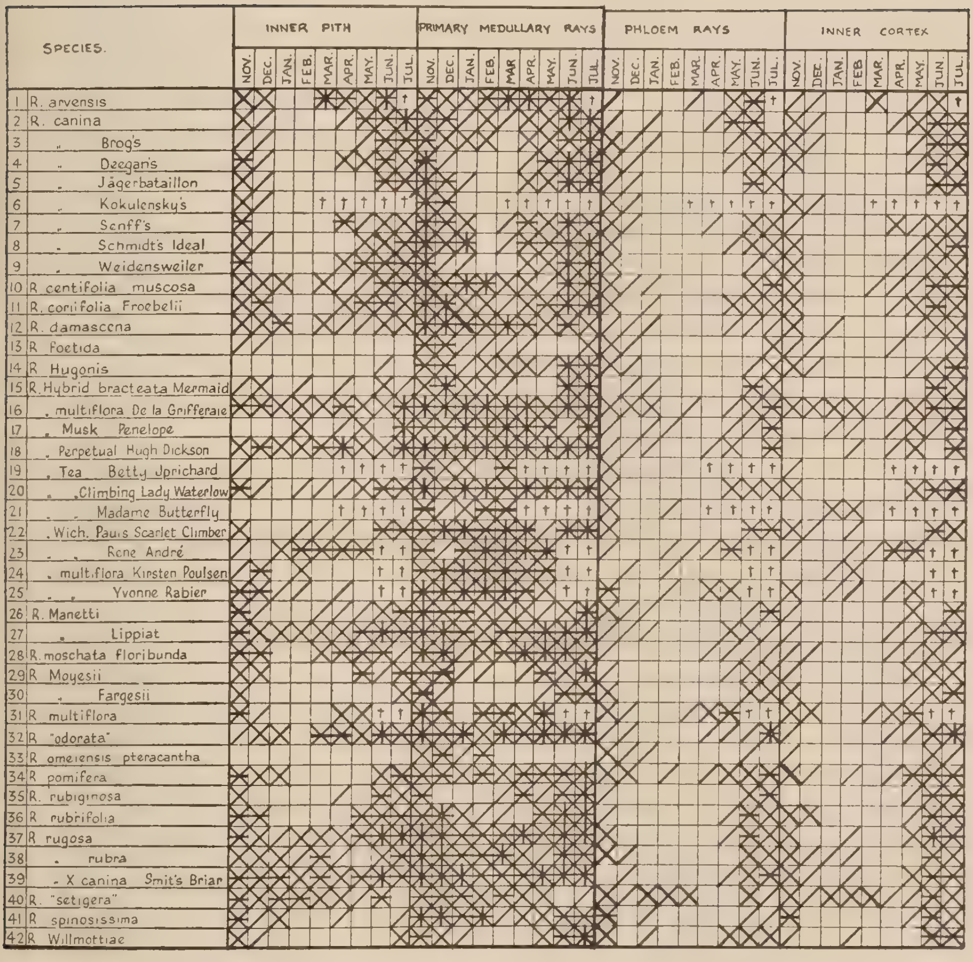
An arbitrary grading of starch content was adopted and is illustrated in Table IV, in which the four principle tissue groups were selected to show the fluctuations of starch over the given period. It can be seen that related species show similar fluctuations, thus constituting another genetically related phenomenon among the species in the genus. The following groups may be drawn up from a consideration of the results in Table IV.

Group A. Those with abundant starch throughout the winter.

R. damascena.
R. H. Musk. Penelope.
R. H.P. Hugh Dickson.
R. H. *multiflora.* Kirsten Poulsen.
R. H. *multiflora.* Yvonne Rabier.
R. multiflora. De la Grifferaie.
R. " odorata "
R. rugosa.
R. rugosa rubra.
R. rugosa × canina. Smit's Briar.

TABLE IV.

Starch Fluctuations in Four Tissues.



KEY TO TABLES IV AND V.

Density of Starch

Packed (e.g. Medullary Rays in Figure A)
Abundant (e.g. Outer Pith in Figure B)
Frequent (e.g. Inner Cortex in Figure D)
Occasional (e.g. Phloam parenchyma in Figure C)
Absent (e.g. Xylem parenchyma in Figure E)
† No material available

R. H.T. Climbing Lady Waterlow.	*R. " setigera ".*
R. H.W. Paul's Scarlet Climber.	*R. spinosissima.*
R. Manetti var. *Lippiat.*	

Group B. Those with starch tending to disappear in the winter.

R. arvensis.	*R.* H.T. Betty Uprichard.
R. canina.	*R.* H.T. Madame Butterfly.
R. coriifolia Froebelii.	*R.* H.W. René André.
R. foetida.	*R. moschata floribunda.*

Group C. Those with little or no starch throughout the winter.

R. canina. Brog's Strain.	*R.* H. *bracteata.* Mermaid.
R. ,, Deegan's Strain.	*R. Moyesii.*
R. ,, Jägerbataillon Strain.	*R. Moyesii Fargesii.*
R. ,, Kokulensky's Strain.	*R. omeiensis pteracantha.*
R. ,, Senff's Strain.	*R. rubiginosa.*
R. ,, Schmidt's Ideal Strain.	*R. rubrifolia.*
R. ,, Weidensweiler Strain.	*R. Willmottiae.*

It is noticeable that closely related species fall into the same groups, except in such highly hybridized subjects as the Hybrid Teas and Hybrid *Wichuraianas.*

The starch content shows no apparent correlation with the habit of the plant, as the " strong growers " of the nurseryman's catalogue appear in all groups.

Starch depletion continued for a longer period in roses than in apples, in most cases till March. There followed a steady rise, and this showed no signs of ceasing when the experiment terminated in July. This applies only to second year wood of the rose. In the apple, there is a complete disappearance in May in the young shoots (Swarbrick (15)), and Smyth (13) also gives the minimum starch period in June for first year shoots. A further point of dissimilarity is found in the fact that several rose species entirely lose their starch in winter, but in the apple, this never happens (Smyth (13, 14) and Kraybill, Sullivan and Miller (12)).

As mentioned earlier, it has been suggested that a high starch content may be correlated with easy rooting of cuttings (Carlson (2)), but the results here obtained tend to disprove such an assertion. If ease of rooting accompanies high starch content, the easy rooters should fall into Group A, and the difficult subjects into Groups B and C. Some of the most easily rooted forms in the foregoing trials were *R. multiflora, R. moschata floribunda,* Paul's Scarlet types of *R. canina,* and *R. rugosa.* These include examples from all three groups. Conversely some of the most difficult to root were *R. Willmottiae, R. coriifolia*

Froebelii and *R. Manetti*, and these again are dispersed throughout the groups. It therefore seems that starch content has no influence on rooting.

To corroborate this conclusion, a further experiment was carried out as follows:—

In April, the four following species were selected:—

1. *R.* "*setigera*" (with abundant starch throughout winter).
2. *R. arvensis* (,, moderate ,, ,, ,,).
3. *R.* "*odorata*" (,, ,, ,, ,, ,,).
4. *R. canina,* Jägerbataillon (with starch disappearing in winter).

One hundred nodal cuttings of each, about eight inches long, were prepared, and were lined out in the open ground. They were taken up and examined in July, and the following percentages of rooted cuttings were found:—

1. *R.* "*setigera*". 0%.
2. *R. arvensis*. 97%.
3. *R.* "*odorata*". 82%.
4. *R. canina,* Jägerbataillon. 92%.

These figures show no correlation with starch content, and it is finally concluded that starch content has no association with ease of rooting in hardwood cuttings.

RELATION OF STARCH CONTENT TO PRUNING.

Arising from the question of seasonal starch fluctuations is the influence of pruning on starch distribution. Three varieties were therefore included in an investigation in which the current year's wood of both pruned and unpruned bushes was examined. The pruned bushes were pruned hard at the beginning of April. Table V shows the relative starch content found.

TABLE V.

Effect of Pruning on Starch Fluctuations.

TISSUE	VARIETY	PRUNED (Current year's wood examined)				UNPRUNED (Current year's wood examined)				UNPRUNED (Previous year's wood examined)			
		APR	MAY	JUN	JUL	APR	MAY	JUN	JUL	APR	MAY	JUN	JUL
Wood	H.T. Lady Inchiquin	t	t	X	X+	t		X+	X	X-	/	X+	X+
	H.T. Shot Silk	t	t	X	X-	t		X-			/	X-	X-
	Pern. Angèle Pernet	t	t	X	X+	t	X	X-	X+	X+	X+	X+	X+
Bast.	H.T. Lady Inchiquin	t	t	X	X+	t		X-	X			X-	X-
	H.T. Shot Silk	t	t	X	X-	t		X-	/			X-	X
	Pern. Angèle Pernet	t	t	X	X+	t	X-	X	X+		/	X-	/

These results show a later accumulation of starch in the pruned bushes, approximately one month behind the unpruned. This was to be expected, as pruning delays growth by about one month. The unpruned bushes show a

drop in starch content in July. Although no examinations were made from August till October, this decrease can be only temporary, as in the previous investigation all species exhibited abundant starch by November. The fall in starch content would seem to be associated with flowering.

The distribution of starch in the previous year's wood from unpruned bushes is similar to that in the wood of the current year, but it does not exhibit the July fall.

From these results it may be concluded that after an initial accumulation, a fall in starch content occurs in the new wood of pruned and unpruned bushes, coinciding with the flowering period, and also that pruning delays the initial starch accumulation.

ACKNOWLEDGMENTS.

The author desires to express her thanks to Prof. R. H. Stoughton for his untiring help, and to Prof. W. B. Brierley for laboratory accommodation and the use of apparatus.

SUMMARY.

A series of experiments was carried out to ascertain the rooting capacities of various species and varieties of the genus Rosa, with variations in the time of insertion and in treatment prior to insertion. Hardwood cuttings were taken at intervals throughout the winter, and the highest rooting percentage was obtained during the period October-December. Softwood cuttings were inserted in the summer, and June was found to be the best time for rooting.

After preparation, the cuttings were subjected to various chemical treatments. Ethylene chlorhydrin, thiourea, sodium nitrate, glucose and the growth hormone β-indolyl-acetic-acid were used in suitable concentrations. β-indolyl-acetic-acid (1 in 10,000 to 1 in 50,000) and glucose (1%) increased the rooting percentage slightly. Ethylene chlorhydrin and thiourea depressed the rooting percentage. No treatment was found to give a pronounced increase or acceleration in rooting.

The effect of the pH value of the solutions used was also considered. Two values were tried, but they had no effect on the subsequent rooting.

Different species and varieties of the genus Rosa showed varying types of starch fluctuation during the season, and may be divided into groups comprising those in which the starch remains throughout the winter, and those in which it disappears. Botanically related species and varieties fall into the same groups, indicating that starch fluctuation is a genetically related phenomenon amongst species of the genus Rosa.

Starch accumulation in the spring is delayed by pruning.

Starch content of the cuttings bears no relation to facility of rooting.

FIGS 1 TO 5.

Transverse sections of Stems (Mid-Internode) in September, showing starch distribution.

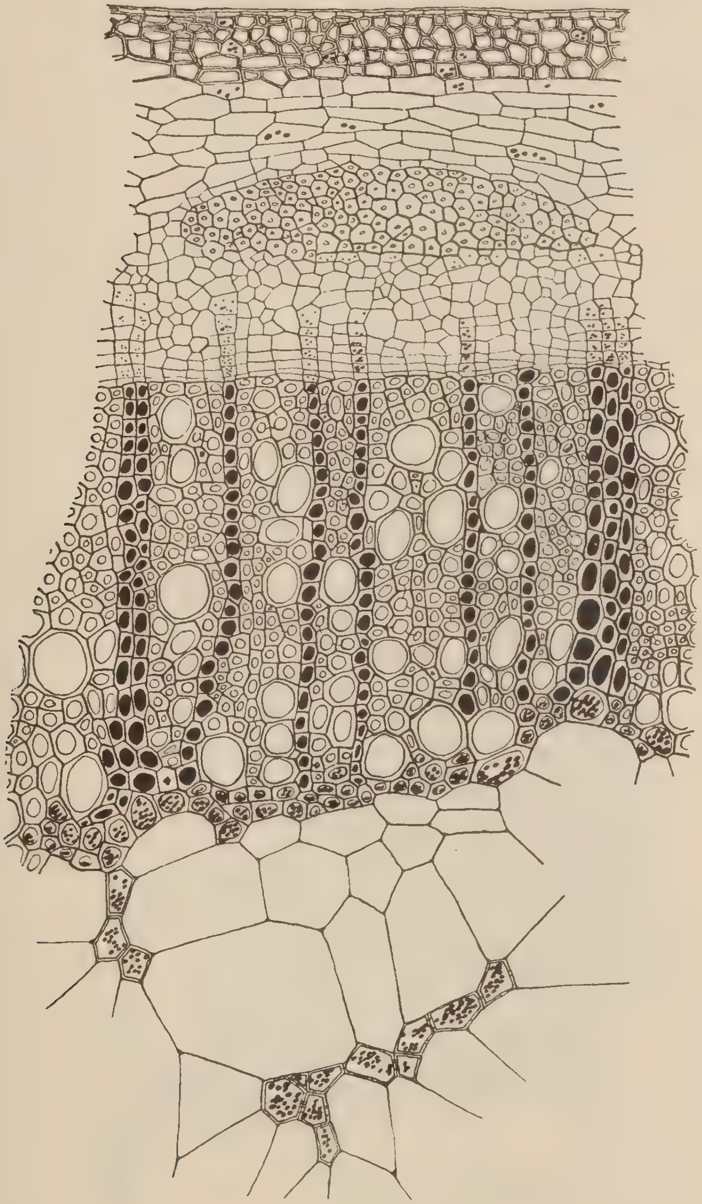


FIG. 1.

Rosa canina (Senff's strain).

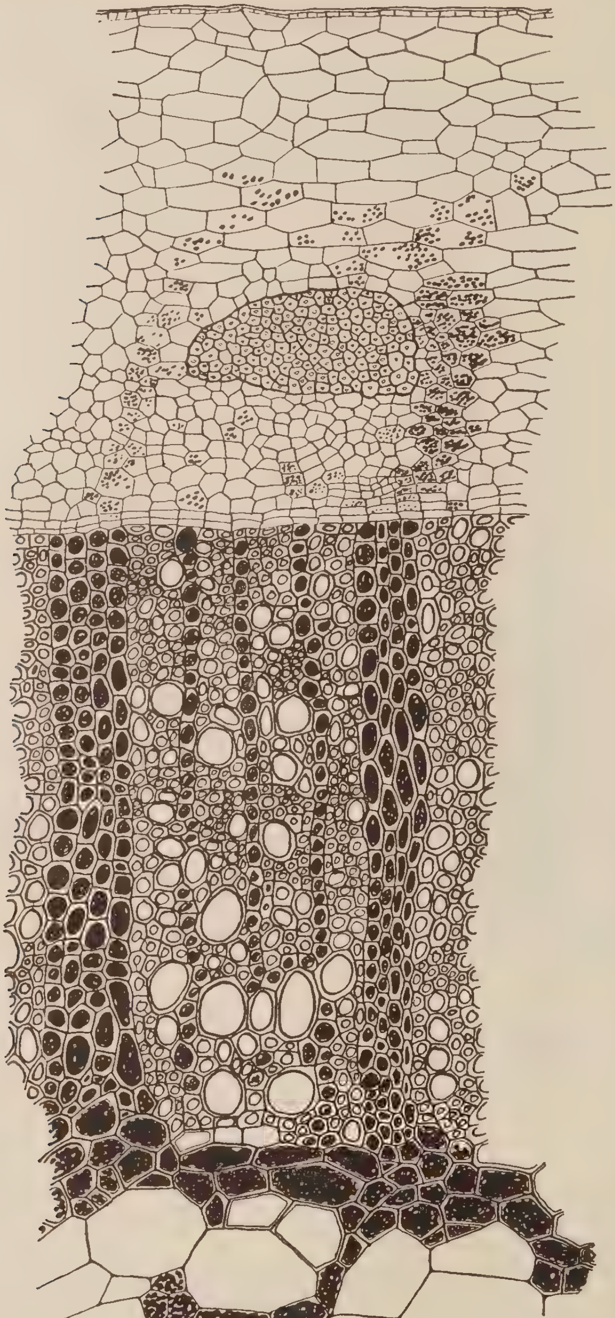


FIG. 2.
Rosa moschata floribunda.

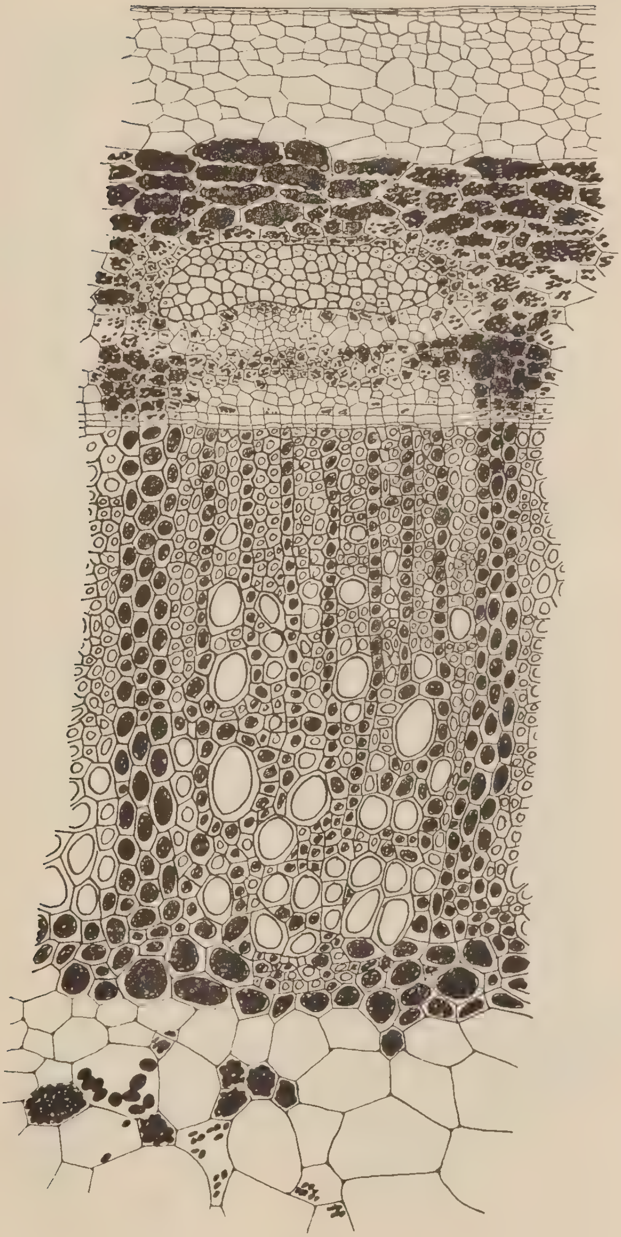


FIG. 3.
Rosa multiflora (Stock).

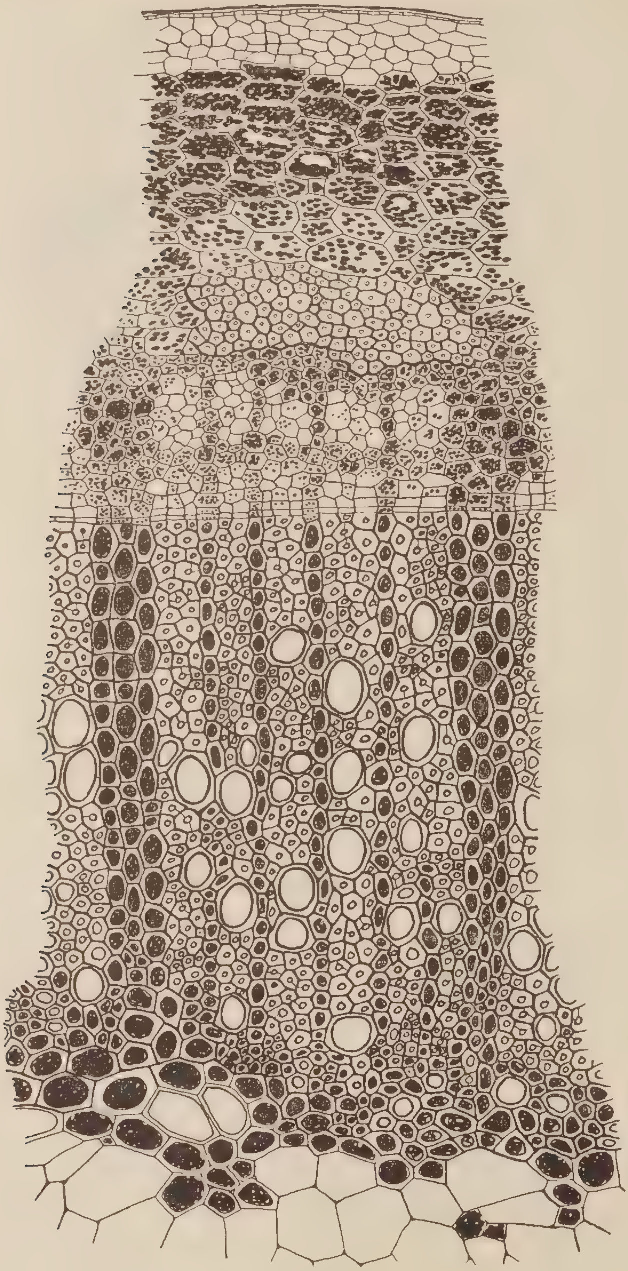


FIG. 4.
Rosa rugosa rubra.

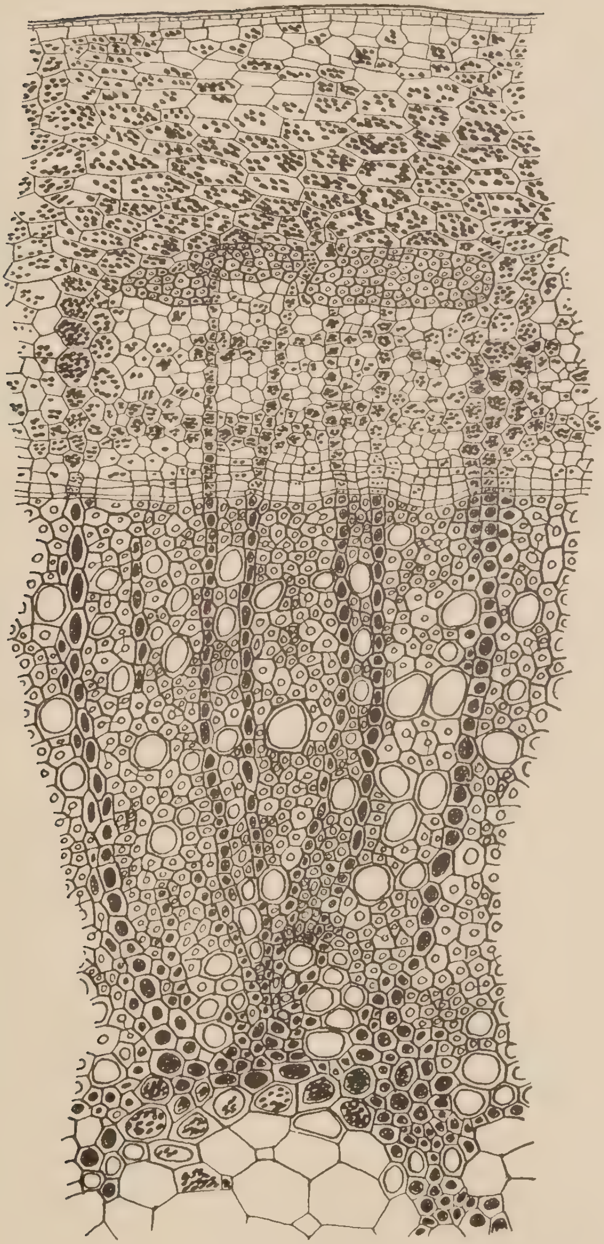


FIG. 5.
Rosa Willmottiae.

LITERATURE REFERENCES.

(1) *Calma, V. C.* and *Richey, H. W.* The influence of amount of foliage on rooting of Coleus cuttings. Proc. Amer. Soc. Hort. Sci., 1930, **27**, 457.

(2) *Carlson, M. C.* Microchemical studies in rooting and non-rooting rose cuttings. Contrib. Boyce Thom. Inst., 1929, **1**, 529.

(3) *Chadwick, L. C.* Influence of position of basal cut on rooting and arrangement of roots on deciduous softwood cuttings. Proc. Amer. Soc. Hort. Sci., 1930, **27**, 487.

(4) ———. Factors influencing rooting of deciduous hardwood cuttings. *Ibid.*, 1931, **28**, 455.

(5) *Denny, F. E.* Chemical treatments for controlling the growth of buds of plants. Boyce Thom. Prof. Paper, 1928, No. 8.

(6) ——— and *Stanton, E. N.* Chemical treatments for shortening the rest periods of pot-grown woody plants. Contrib. Boyce Thom. Inst., 1929, **1**, 355.

(7) *Esper, H. C.* and *Roof, L. R.* Studies in the propagation of softwood cuttings based on temperature, defoliation and kind of media. Proc. Amer. Soc. Hort. Sci., 1931, **27**, 452.

(8) *Ferguson, J.* A botanical study of rose stocks. Journ. Roy Hort. Soc., 1933, **58**, 344.

(9) *Hitchcock, A. E.* and *Zimmerman, P. W.* Rooting of greenwood cuttings as influenced by age of tissue at base. Proc. Amer. Soc. Hort. Sci., 1930, **27**, 136.

(10) ——— and ———. Effect of growth substances on rooting of cuttings. Contrib. Boyce Thom. Inst., 1936, **8**, 63.

(11) *Klein, I.* Stimulative action of chemicals on the rooting of softwood and hardwood cuttings. Proc. Amer. Soc. Hort. Sci., 1930, **27**, 482.

(12) *Kraybill, H. R., Sullivan, J. T.* and *Miller, L. P.* Seasonal changes in composition of Stayman apple trees. I. Carbohydrates. *Ibid.*, 1930, **27**, 206.

(13) *Smyth, E. S.* The seasonal cycles of nitrogenous and carbohydrate materials in fruit trees. Journ. Pom. & Hort. Sci., 1934, **12**, 249.

(14) ———. Seasonal cycles of ash, carbohydrates and nitrogenous constituents in the terminal shoots of apple trees. II. Carbohydrate fractions and lignin. *Ibid.*, 1938, **16**, 185.

(15) *Swarbrick, T.* Studies in the physiology of fruit trees. I. The seasonal starch content and cambial activity in 1-5 year old apple branches. *Ibid.*, 1927, **6**, 296.

(16) *Tincker, M. A. H.* Experiments with growth substances, or hormones, and the rooting of cuttings. Journ. Roy. Hort. Soc., 1936, **61**, 510.

(17) ———. Growth substances and the rooting of cuttings. *Ibid.*, 1938, **63**, 210.

(18) *Yerkes, G. E.* Rose understocks in a 5-year test. Proc. Amer. Soc. Hort. Sci., 1930, **27**, 463.

(*Received* 18/3/39.)

STUDIES ON THE NUTRITION OF TULIPS AND NARCISSI

By C. BOULD
Department of Horticulture, University of Reading*

Introduction.

The nutritional requirements of many plants have been investigated and their deficiency symptoms described, but to the writer's knowledge no extended experiments on this subject have been carried out on bulbs. Since the growing of flowering bulbs now occupies an important place in British horticulture, the time is opportune for such experiments. Those described in the present paper are only of a preliminary nature, but may serve as a basis for further work.

The literature dealing with the nutrition of bulbs is meagre. A small experiment was carried out at Kirton by Handley (6) on tulips a few years ago in which the bulbs were grown in 6 in. pots of sand and given a complete nutrient solution, solutions omitting nitrogen, phosphorus and potassium respectively, and water only. There was little difference between the growth of plants receiving full nutrient solution and those not receiving potassium ; that of plants not receiving phosphorus was definitely poor, whilst plants receiving the solution without nitrogen were weak and spindly.

The published results of field manurial trials are conflicting. This, however, is to be expected when the various soil types on which bulbs are grown are considered. Gibson (5), in a paper on the manuring of bulbs, sums up the position in the following words: " Deep cultivation and a suitable rotation will pay bigger dividends at present than the manurial mixtures sold under the name of bulb fertilizers."

The investigations to be outlined here were designed to obtain information on the effect of nutritional deficiencies on the growth, flowering and bulb weight increase of Narcissi and tulips, and also on the chemical composition of the bulbs. Studies were also made of the rate of respiration of the bulbs during the so-called " dormant " or storage period.

Experimental Method.

Owing to the nature of the plants and the number intended for use in the experiment, some form of container for the sand, other than pots, was desirable. It was decided to grow the bulbs in silver sand in a series of rectangular compartments made of galvanized iron, and sunk into the ground as a protection

* Now at University College of North Wales, Bangor.

against rapid fluctuations in temperature. The arrangement was not entirely satisfactory and for further experiments a different one was adopted which will be described later.

The compartments, ten in number, were constructed in two blocks of five each, the size of the individual compartments being 4 ft. 3 in. long, by 1 ft. 9 in. wide, by 1 ft. 6 in. deep.

A plot of land 22 ft. 3 in. by 4 ft. 6 in. was marked out and excavated to a depth of 1 ft. 9 in. at one end and 2 ft. 1 in. at the other. Eight brick bases were then built, on which to rest the walls of the compartments. A layer of clinkers was placed in the bottom, followed by coarse ashes and then fine ashes, until the level of the brick bases was reached. Wire netting ($\frac{1}{2}$ in. mesh) was laid over the ashes, and the walls of the compartments were then placed in position (Plate I, Fig. 1). Connection was made between the lower end of the pit and a land drain for drainage purposes. After thoroughly leaching the ashes with water the compartments were filled to a depth of 10 in. with grade 20a of medium silica sand, supplied by Messrs. Joseph Arnold & Son, Leighton Buzzard. The sand was then thoroughly leached and the surfaces levelled and marked out for planting.

The bulbs were obtained from Spalding, Lincolnshire. The Narcissi (variety King Alfred) were all "tight double nosed" bulbs and had been given the standard hot water treatment before dispatch. The tulips (variety Farncombe Sanders) were 12 cm. (circumference) bulbs.

Ten lots of Narcissi, and 10 of tulips, each consisting of 20 bulbs, were chosen, and, after removing all loose "skins" and roots, were weighed to the nearest gramme. One lot of Narcissi, and one of tulips was planted in each compartment, the Narcissi towards the middle and the tulips towards the outside of the double block of compartments (Plate I, Fig. 2). The bulbs were planted in rows of 10, 4 rows per compartment, the distance apart of the bulbs between and within the rows being 5 in. In all, 400 bulbs were used, consisting of equal numbers of Narcissi and tulips. They were covered with 5 in. of sand, thus leaving 3 in. between the top of the compartments and the level of the sand.

TREATMENTS.

The five treatments employed were:—

Complete nutrient solution	(N.P.K.)
,, ,, minus potassium ..	(N.P.)
,, ,, ,, phosphorus ..	(N.K.)
,, ,, ,, nitrogen ..	(P.K.)
Water only (Control).	

In the first year the experiment was considered as two randomized blocks, the arrangement of the treatments within the blocks being as shown below.

N.K.	N.P.	P.K.	N.P.K.	Control.
N.P.	Control.	N.P.K.	N.K.	P.K.

Nutrient solutions.—The composition of the complete nutrient solution was that recommended by Wallace (12) and contained the following salts:—

Potassium nitrate (KNO_3)	6·0 gm.
Calcium nitrate ($Ca(NO_3)_2 \cdot 4H_2O$)	1·4 ,,
Dipotassium hydrogen phosphate (K_2HPO_4) ..	1·0 ,,
Calcium sulphate ($CaSO_4 \cdot 2H_2O$)	2·0 ,,
Magnesium sulphate ($MgSO_4 \cdot 7H_2O$)	3·0 ,,
Sodium chloride (NaCl)	0·5 ,,
Ferric chloride (Fe_2Cl_6)	0·4 ,,
Water, to	1,000 cc.

One litre of this stock solution was diluted with water to 10 litres for use.

In the "minus" solutions, sodium was substituted for the base and sulphate for the acid radical, in equivalent amounts. The sodium and potassium phosphates were made up as separate stock solutions and added during dilution.

Owing to the large quantities of solution required and to the absence of facilities for collecting and storing rain water, tap water was used for diluting the stock solutions and for watering the plants. The effect of tap water on the reaction of the solutions will be discussed later.

The solutions were applied once a week at the rate of 5 litres per compartment. Water was given at the same rate when necessary. Before every fourth application of nutrient solution the sand was thoroughly leached with water to prevent the accumulation of unabsorbed ions.

In addition to the above, a solution having the following composition, but diluted to 1/100 before use, was given once in four weeks to supply the "minor" essential elements:—

Copper sulphate ($CuSO_4 \cdot 5H_2O$)	0·10 gm.
Manganese sulphate ($MnSO_4 \cdot 7H_2O$)	0·10 ,,
Boric acid (H_3BO_3)	0·11 ,,
Water, to	1,000 cc.

B.D.H. salts were used throughout for making up the solutions.

GROWTH AND DEVELOPMENT OF THE PLANTS.

Tulips, 1934-5.

Foliage and growth characteristics.—The tulips were planted on November 1st, 1934. The first shoots appeared on February 19th, 1935, and all were showing on March 1st. During the first year, treatment had no effect on the date of appearance of the shoots.

The growth of the plants receiving the complete solution, and of those not receiving potassium, was good, little or no difference being discernible. The leaves were large and dark green, and although slight marginal chlorosis developed in the plants not receiving potassium, this was not followed by any leaf scorch.

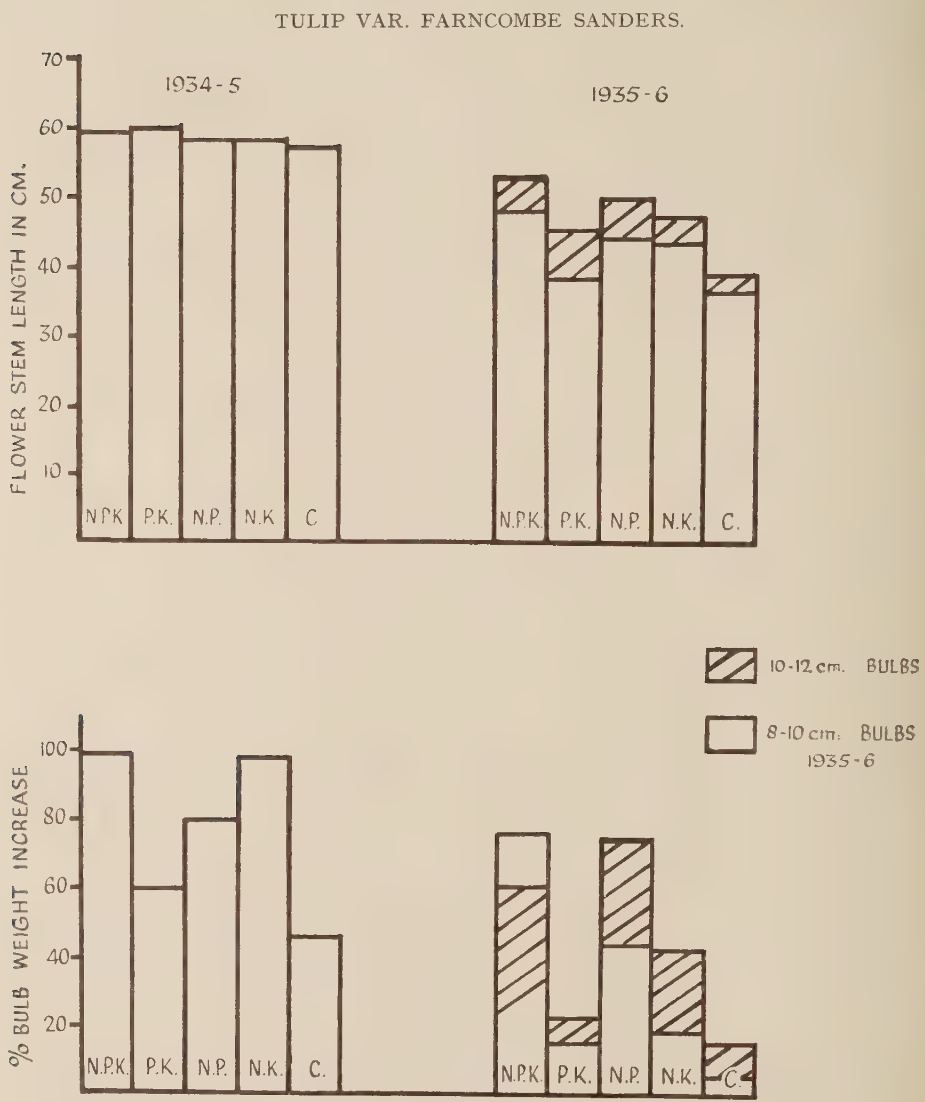
The plants not receiving phosphorus did not make quite such good growth, but the difference was not pronounced. The leaves were bluish green in colour and developed slight purplish tints before death.

The growth of the plants without nitrogen, and with water only, was much inferior. The leaves were smaller, more upright in growth and yellowish green in colour. In both cases the leaves developed reddish tints before death, the colour first developing around the margins and towards the apex. The flower stems, particularly at the base, also developed reddish tints. These symptoms are typical of nitrogen starvation.

Flower stem length.—The flower stems were measured twice, once before flowering and again when the flowers were showing full colour. The data for the latter record are presented in the form of a histogram in Text Fig. 1. Owing to competition between plants within the same compartment, each plant, from a statistical point of view, cannot be treated as an individual ; hence in the analysis of the results only the mean flower stem length for each compartment has been used. From the analysis of variance (omitted here), "z" for treatments$=0{\cdot}7597$; and for $P=0{\cdot}05$, "z"$=0{\cdot}9272$. Treatments therefore had no significant effect on flower stem length during the first year.

Flowers.—In the first season the treatments had no effect on the date of flowering and only a small effect on the size and quality of the flowers, the flowers of plants not receiving nitrogen, and of plants receiving water only, being slightly smaller. Omission of potassium had no effect on the size or quality of the flowers.

Bulb weight increase.—Omission of nitrogen and of potassium, or of all nutrients, resulted in a significantly lower bulb weight increase as compared with full nutrient treatment. Omission of phosphorus had no significant effect on bulb weight increase.



TEXT FIG. 1.

Effect of treatments on flower stem length and bulb weight increase.

Tulips, 1935-6.

Foliage and growth characteristics.—The treatments were not replicated in this, the second, year, all the tulip bulbs being planted in one block of compartments and the Narcissi in the other block. The tulip bulbs were divided into two

lots, (1) including bulbs from 10 to 12 cm. in circumference, and (2) bulbs varying from 8 to 10 cm. One sample (20 bulbs) from each lot was planted per compartment. The bulbs were planted on October 12th, 1935.

The shoots in this year were much later in appearing than in 1935. The first shoots appeared on March 10th, almost three weeks later than in the previous year. Omission of nitrogen, or of all nutrients, delayed the appearance of the shoots.

The foliage characteristics were similar to those of the previous year, except that the differences were more marked. Again, there was little difference in the appearance of plants receiving full nutrient treatment and those without potassium. This was an unexpected result since the potassium content of the plants must have been considerably reduced. The first year's treatment, indeed, reduced the potassium content of the bulb from 1·706% to 0·917% (as % of dry weight).

Omission of phosphorus began to show an effect during the second year. Growth was reduced, the leaves were smaller and bluish green in colour, and they developed more intense purplish red tints before death.

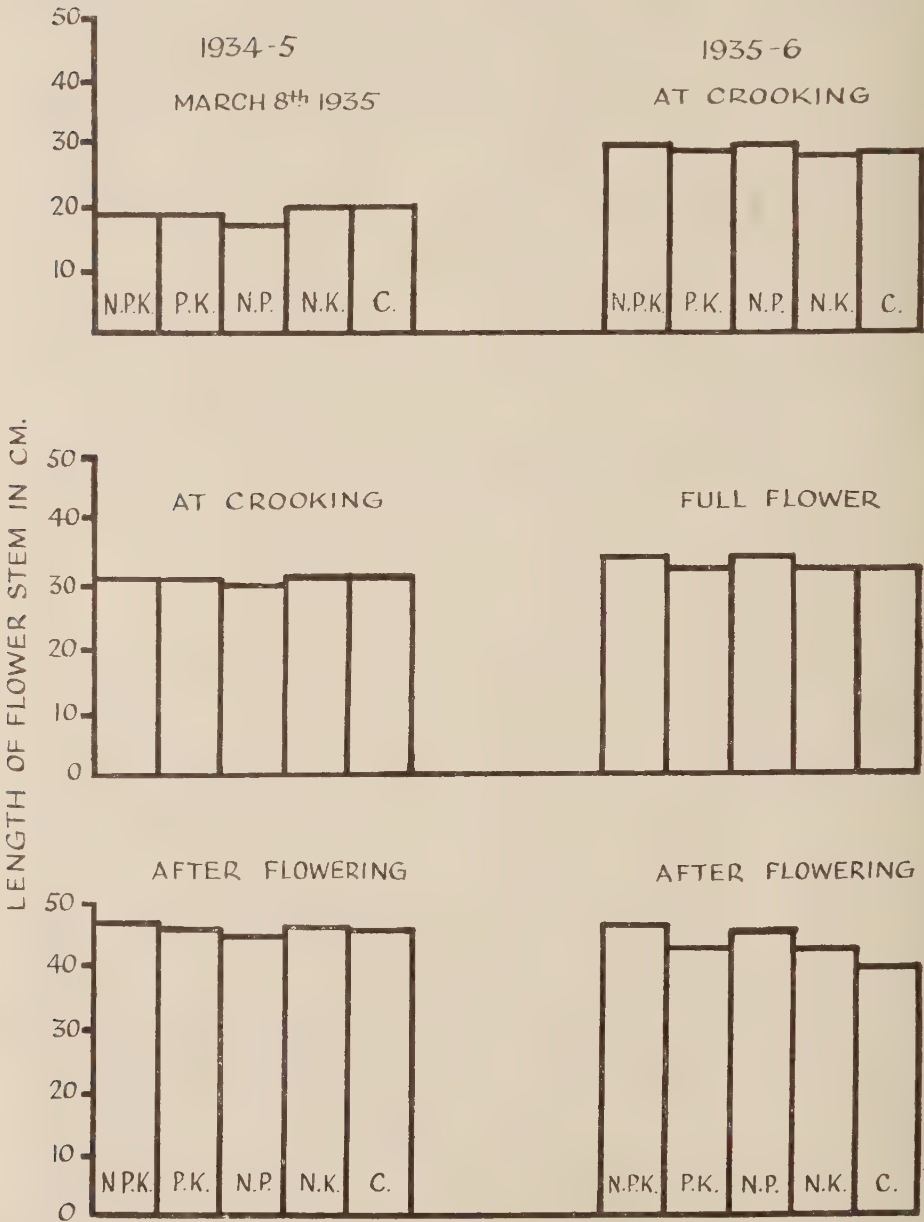
The growth of the plants in the absence of nitrogen, and with water only, was very poor. The leaves were small, pale yellowish green in colour, and they began to develop reddish tints about the beginning of May.

During this year it was noticed that the plants in the minus-nitrogen and water-only treatments near the edges of the compartments made better growth than those in the middle. (Plate II, Figs. 4 and 7.) Evidently these plants must have been obtaining some solution from the neighbouring compartments. Unfortunately this was not noticed until the second year and could not therefore be remedied, but for later experiments the bottom of the compartments was concreted, leaving a small strip 3 ft. by 2 in. uncemented in the middle of each compartment, for drainage.

Flower stem length.—Omission of nitrogen, and of all nutrients, considerably reduced the flower stem length. Omission of phosphorus caused less reduction, whilst omission of potassium had the least effect (Text Fig. 1).

Flowers.—The minus-nitrogen and water-only treatments delayed flowering by about three days. There were marked differences in flower quality during this year. The full nutrient and minus-potassium treatments produced the best blooms, the former producing slightly larger and more uniform flowers than the latter, but the omission of potassium did not affect the colour of the flowers. Omission of phosphorus reduced the size of the flowers slightly. The flowers of the plants without nitrogen, and with water only, were definitely poorer. They were much smaller and lighter in colour than the others, and were the first to shed their petals. None of the treatments produced blooms of so high a quality as in the previous year.

NARCISSUS VAR. KING ALFRED.



TEXT FIG. 2.
Effect of treatment on flower stem length.

Bulb weight increase.—All treatments gave a lower bulb weight increase as compared with full nutrient treatment. Omission of phosphorus had a marked detrimental effect during the second year. Omission of potassium had the least effect. (Text Fig. 1.)

In the first year, the treatments had little effect on the size of the bulbs ; but in the second year, omission of nitrogen, and of phosphorus, or of all nutrients, considerably reduced the percentage of bulbs over 10 cm. in circumference. Omission of potassium had the least effect.

Narcissus, 1934-5.

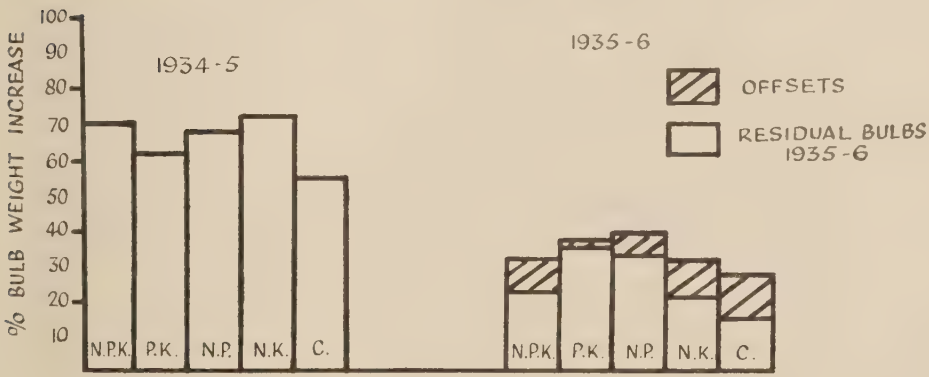
Foliage and growth characteristics.—The bulbs were planted on November 1st, 1934. The first shoots appeared on January 1st and all were showing on January 18th. Omission of nitrogen delayed the appearance of the shoots by a few days.

The general growth of the plants under all treatments was very similar throughout this, the first, year, although towards the end of the growing season the plants without nitrogen, and those with water only, appeared to be less vigorous and paler green in colour than the others.

Flower stem length.—Data on flower stem length are given in Text Fig. 2, which shows the mean flower stem length for plants having two flowers only. Treatments had no significant effect on flower stem length.

Flowers.—In this season the treatments had no effect on the time of flowering or on the quality of the flowers.

NARCISSUS VAR. KING ALFRED.



Text Fig. 3.
Effect of treatment on bulb weight increase.

Bulb weight increase.—During this year omission of nitrogen, and of all nutrients, resulted in a significantly lower bulb weight increase as compared with full nutrient treatment. Omission of potassium, or of phosphorus, had no significant effect. (Text Fig. 3.)

Narcissus, 1935-6.

Foliage and growth characteristics.—In this, the second, year, the bulbs were divided into two grades, (1) residual bulbs (that portion of the mother bulb which remained after the removal of the offsets) and (2) large offsets. Twenty bulbs of each grade were planted in each of five compartments. There was no replication of the treatments.

Omission of nitrogen, phosphorus, and potassium, and of all nutrients delayed the appearance of the shoots by a few days. The plants with complete solution made the best growth, whilst the omission of potassium had the least detrimental effect. No marked deficiency symptoms could be observed, although the leaves of the plants not receiving nitrogen and those of the plants receiving water only, were paler green in colour.

The general growth of the plants was definitely poorer than in the previous year. The reason for this reduced growth is not understood. Possibly the plants were receiving insufficient nutrient solution, and this, coupled with the high reaction of the solutions, would partly account for the poor growth.

Flower stem length.—Omission of nitrogen, phosphorus, and of all nutrients, reduced the flower stem length. Omission of potassium had the least effect. (Text Fig. 2.)

Flowers.—Omission of nitrogen, and of all nutrients, delayed flowering by a few days. There were only small differences in the quality of the flowers. The flowers of plants not receiving nitrogen, and those receiving water only, appeared to be slightly paler in colour, and the perianth of less substance. No difference could be observed between the other treatments.

Bulb weight increase.—The percentage bulb weight increase figures for this year were all very low, indicating that the conditions were unsuitable for normal growth. (Text Fig. 3.) It is unwise, therefore, to attach significance to these figures.

Further Experiment with Narcissi.

The poor growth of the Narcissi in the experiments just described may have been due to several causes, of which insufficient nutrient supply, wrong nutrient balance, and a high pH are the most probable. The stock nutrient solutions were diluted with tap water, and on testing the reactions of the solutions it was found that they varied between pH 7 and pH 8. It is known that some plants

do not make good growth in nutrient solutions on the alkaline side of neutrality. This is partly due to the effect on the rate of absorption and to the precipitation of certain ions from solution. The following experiment was designed to study the effect of potassium on the growth of Narcissi in more detail, and at the same time to see if the reaction of the nutrient solutions was partly responsible for the poor growth.

The previous experiments showed that omission of potassium from the nutrient solution did not produce any noticeable effect on the intensity of the flower colour during the first year. This finding is contrary to general opinion, which is based on the results of field experiments and analogy with the response of other plants to potash manuring. Hill and Davis (7), working with Chrysanthemums in sand culture, found that a deficiency of potassium not only produced marked foliage symptoms but also affected the intensity of the flower colour. It must be borne in mind, however, that bulbs start with a large reserve of food material and minerals which might delay for some time the onset of deficiency symptoms.

Since variations in the intensity of yellow are difficult to assess, a variety of Narcissus possessing more colour was used for this experiment, viz. " Bath's Flame ".

TREATMENTS.

The six treatments were :—

Complete nutrient solution adjusted to pH 5
,, ,, ,, ,, ,, ,, 6
,, ,, ,, ,, ,, ,, 7
Complete nutrient minus potassium ,, ,, 5
,, ,, ,, ,, ,, ,, 6
,, ,, ,, ,, ,, ,, 7

The composition and concentration of the solutions were the same as those used for the previous experiments, and the reactions were adjusted by the addition of sulphuric acid, which slightly altered the concentration of the sulphate ions. Each treatment was replicated four times.

EXPERIMENTAL METHOD.

The bulbs were planted on October 27th, 1936, in silver sand contained in galvanized iron bins, sunk in specially prepared trenches. The bins were 15 in. in diameter and 17 in. deep. Holes were drilled in the bottom of each bin for drainage, and the bins were then placed in the trenches on a layer of sand followed below by fine ashes and then clinkers. The trenches were connected by a common channel to a land drain.

The experiment was laid out in the form of four randomized blocks, A, B, C and D, each block or trench containing six bins. The construction of the trenches and the general layout are shown in Plate III, Fig. 8. Ten double nosed bulbs were planted in each bin, 5 in. deep. Each bin received 5 litres of nutrient solution per week until the plants were some 6 in. high, when the applications were given twice weekly. The routine treatment was the same as in the previous experiment.

General growth and flower quality.

The treatment had no effect on the date of appearance of the shoots, nor could any difference be observed in the general growth of the plants throughout the season. All the bulbs flowered at approximately the same time, and no difference could be observed in the intensity of the flower colour or in the quality of the blooms.

Bulb weight increase.

The percentage bulb weight increase for each plot is given in Table I, and the mean percentage bulb weight increase of four plots is given in Table II.

TABLE I.

Treatments.	A.	B.	C.	D.	Total.	Mean.
N.P.K. pH 5 ..	73	64	67	54	258	64·50
,, pH 6 ..	70	67	69	63	267	67·25
,, pH 7 ..	66	65	67	67	265	66·25
N.P. pH 5 ..	53	54	46	55	208	52·00
,, pH 6 ..	57	55	60	43	215	53·75
,, pH 7 ..	58	57	58	49	222	55·50
Total	377	362	367	331	1,437	
Mean	62·833	60·333	61·166	55·166		59·875

Analysis of variance.
Percentage bulb weight increase.

Variance due to	Degrees of freedom.	Sum of squares.	Mean square.	$\frac{1}{2}\log_e \sigma^2$
Blocks	3	196·80	65·60	2·0918
Treatments ..	5	940·38	188·07	2·6185
Error	15	297·45	19·80	1·4927
		1,434·63		

The value of "z" for treatments = 1·1256. For P = 0·05, "z" = 0·5326.

Table II.

Percentage bulb weight increase. Mean of four plots.

N.P.K. pH 5.	N.P.K. pH 6.	N.P.K. pH 7.	N.P. pH 5.	N.P. pH 6.	N.P. pH 7.	General mean.	S.E.	Significant difference.
64·50	67·25	66·25	52·00	53·75	55·50	59·875	2·22	7·70

The figures thus show that the treatments have had a significant effect on bulb weight increase. Omission of potassium had a significant adverse effect on bulb weight increase, but the reaction of the solution had no significant effect.

Methods of Sampling and Chemical Analysis.

Chemical analyses were made of the original bulbs in the first experiment and of the bulbs at the end of the first year of treatment.

Separate samples were taken for carbohydrate and inorganic analyses, and since the samples were taken on different dates the material is not strictly comparable. Dates of sampling are given in the tables of results.

Carbohydrates.

Sampling and Preservation of samples.—Random samples consisting of six bulbs of Narcissus and ten of tulip were used for analysis. After removing loose "skins" and roots the bulbs were chopped into small pieces and thoroughly mixed ; samples of about 20 gm. were then weighed out as quickly as possible. Duplicate samples were taken in each case.

After weighing, the samples were dropped into sufficient boiling 95% alcohol to give a final concentration of about 80%, allowing for the water in the tissue. The samples were boiled for 10 minutes under a reflux condenser to inactivate the enzymes, and then transferred to bottles which were tightly corked. No calcium carbonate was added, since Archbold (1) and Denny (2) have shown that the addition of calcium carbonate to alcoholic solutions does not neutralize acidity. The writer found that no reducing sugars were present in samples of peas stored in alcohol to which no calcium carbonate had been added. It is reasonable, therefore, to infer that no inversion of disaccharide occurs during storage in un-neutralized alcohol, or during distillation, provided the temperature does not rise above 60° C. (reduced pressure).

Extraction of sugars.—The alcohol from the preserved samples was filtered through a dry, weighed, extraction thimble into a 250 cc. volumetric flask. The solid material contained in the thimble was then extracted in a Soxhlet extraction apparatus for 8 hours with approximately 100 cc. of 80% alcohol. The extracts were combined and made up to 250 cc.

Alcohol soluble material.—A 25 cc. aliquot part of the alcohol extract was evaporated on a steam bath, dried and weighed.

Alcohol insoluble matter.—After the extraction with alcohol the thimble containing the insoluble residue was dried and weighed. Total dry matter was obtained by the addition of these two values.

Distillation.—In order to avoid any possible inversion of sucrose, the alcoholic extract was distilled under reduced pressure at a temperature of about 60° C. until some 10-20 cc. remained. This residue was taken up in boiling water and transferred to a 250 cc. flask.

Clearing.—5 cc. of a saturated solution of neutral lead acetate were added and the contents of the flask rotated gently. After standing for about 15 minutes the extracts were filtered through a Whatman No. 541 filter paper on to about 0·5 gm. of solid potassium oxalate, to precipitate the excess lead, and the precipitate was washed well with hot water. After standing several hours, the liquid was filtered through a Whatman No. 40 filter paper into a 500 cc. volumetric flask and made up to this volume.

Estimation of sugars.—Shaffer and Hartmann's (10) "macro" method (cuprous titration) was used for the estimations. Reducing and invert sugars were estimated on 50 cc. aliquot parts. Consistent results were obtained by this method.

For the estimation of total sugars, 100 cc. of the cleared solution were pipetted into a boiling flask, 5 gm. of citric acid crystals added, the solution brought to the boil and boiled under a reflux condenser for 10 minutes, cooled, neutralized with 5N. caustic soda, and made up to 250 cc. Two 50 cc. portions of this solution were used for the estimation of reducing sugars. The difference in reducing power before and after inversion was assumed to be due to the inversion of disaccharides, probably sucrose.

Starch.—The methods for starch determination are all open to criticism. (See Smyth (11) and Denny (3).) The method used in the present work was chosen because it eliminated the use of acid hydrolysis, and because it gave a very good percentage recovery when using known amounts of purified B.D.H. potato starch.

The dry, alcohol insoluble residue was ground until it would pass through a 60 mesh sieve. After drying, samples of about 0·8 gm. were weighed out into 200 cc. Erlenmeyer flasks, 50 cc. of distilled water added, the flasks plugged with cotton wool, and then placed in an autoclave for 1 hour at 120° C. This was necessary, since boiling alone did not break up all the cells. After autoclaving, the samples were cooled, water was added up to 100 cc. and they were then treated with malt diastase following the method of Walton and Coe (13). After clearing, as for sugars, the reducing power, due to maltose, was estimated by Shaffer and Hartmann's method, and the amount of glucose calculated by means of a conversion graph, as recommended by Gardner (4).

Inorganic analyses.

Twelve Narcissus and 15 tulip bulbs were taken from each treatment as samples for analysis. After removing loose "skins" and roots, the bulbs were chopped into small pieces, 20 gm. samples taken for dry weight determinations, and the remainder dried. After drying, the samples were ground till they passed through a 40 mesh sieve. Samples were analysed for ash, total nitrogen, phosphorus and potassium.

Ash and total potassium.—10 gm. samples of oven dry material were weighed out into silica dishes and ashed over a Bunsen flame. After weighing, the ash was dissolved in hydrochloric acid, evaporated to dryness, and gently heated for an hour to dehydrate the silica. The residue was taken up in dilute hydrochloric acid and filtered into a 500 cc. volumetric flask. After precipitating sulphates as barium sulphate, potassium was estimated in the filtrate by the perchlorate method as described by Morris (8).

It was intended to estimate phosphorus in the same solution, but it was found that the values so obtained were considerably lower than those obtained by a wet digestion method, indicating a loss of phosphorus during ashing.

Phosphorus.—Ashing the dry matter after treating with magnesium nitrate solution, and oxidation of the organic matter with a mixture of concentrated sulphuric and nitric acids, gave comparable results. Phosphorus was estimated gravimetrically as strychnine phosphomolybdate, following the method described by Peters and Van Slyke (9).

Total nitrogen.—This was estimated by the Kjeldahl method.

RESULTS.

The results of the analyses are contained in Tables III to VI, and will be discussed later. (See p. 271.)

TABLE III.

Organic composition of tulip bulbs, var. Farncombe Sanders, before and after treatment.

Date sampled.	Treatments.	Percentage of: Alcohol sol. mat.	Total dry weight.	Reducing sugars.		Total invert sugars.		Starch.	
		Fresh weight.	Fresh weight.	Fresh weight.	Dry weight.	Fresh weight.	Dry weight.	Fresh weight.	Dry weight.
11–12–34	Orig. bulbs	10·74	42·99	0·40	0·94	7·77	18·08	22·55	52·46
23–7–35	N.P.K.	3·98	41·71	0·20	0·47	2·47	5·94	29·71	71·22
,,	P.K.	3·93	43·15	0·23	0·54	2·76	6·41	31·18	72·26
,,	N.K.	4·09	42·46	0·25	0·59	2·89	6·80	29·72	70·00
,,	N.P.	4·96	43·58	0·33	0·77	3·63	8·34	30·06	68·97
,,	H_2O.	5·23	43·84	0·23	0·53	4·03	9·14	30·75	69·78

TABLE IV.

Organic composition of Narcissus bulbs, var. King Alfred, before and after treatment.

Date sampled.	Treatments.	Percentage of Alcohol. sol. mat. Fresh weight.	Total dry weight. Fresh weight.	Reducing sugars. Fresh weight.	Reducing sugars. Dry weight.	Total invert sugars. Fresh weight.	Total invert sugars. Dry weight.	Starch. Fresh weight.	Starch. Dry weight.
11–12–34	Orig. bulbs	7·08	35·75	0·51	1·43	3·89	10·88	17·03	47·63
23–7–35	N.P.K.	3·90	34·78	0·26	0·76	2·31	6·64	19·76	56·68
,,	P.K.	3·96	35·57	0·23	0·65	2·35	6·61	20·10	57·60
,,	N.K.	4·23	33·08	0·26	0·78	2·42	7·28	18·80	56·80
,,	N.P.	4·29	33·59	0·32	0·96	2·46	7·32	18·29	54·40
,,	H_2O.	4·43	33·86	0·54	1·62	2·59	7·66	18·47	54·52

TABLE V.

Inorganic composition and total nitrogen content of tulip bulbs, var. Farncombe Sanders, before and after treatment.

Date sampled.	Treatments.	Dry weight as % of fresh weight.	As % of dry weight. Ash.	N.	P_2O_5.	K_2O.
11–12–34	Original bulbs ..	42·99	3·425	2·030	0·623	1·802
7–11–35	N.P.K.	42·06	2·91	1·302	0·385	1·706
,,	N.P.	43·01	1·73	1·354	0·395	0·917
,,	P.K.	45·76	2·55	0·882	0·431	1·529
,,	N.K.	43·23	2·42	1·225	0·253	1·579
,,	H_2O.	45·36	1·80	0·906	0·345	0·982

TABLE VI.

Inorganic composition and total nitrogen content of Narcissus bulbs, var. King Alfred, before and after treatment.

Date sampled.	Treatments.	Dry weight as % of fresh weight.	As % of dry weight. Ash.	N.	P_2O_5.	K_2O.
11–12–34	Original bulbs ..	35·75	3·23	1·884	0·448	1·313
12–10–35	N.P.K.	36·54	2·54	1·225	0·296	1·119
,,	N.P.	34·33	2·14	1·295	0·307	0·816
,,	P.K.	34·71	2·68	0·988	0·316	1·207
,,	N.K.	34·76	2·56	1·204	0·254	1·163
,,	H_2O.	35·87	1·94	1·001	0·272	0·704

RESPIRATION STUDIES ON BULBS.

The experiments now to be described were carried out for the purpose of obtaining information on the general trend of respiration during the storage period of the bulb, and to investigate any possible effect that a particular treatment during the previous growing season might have on the rate of respiration. Since the study constituted only a sideline of the main investigations, the method used was not elaborate, and it was possible to measure only the amount of carbon dioxide given off by the respiring bulbs.

Experimental method.

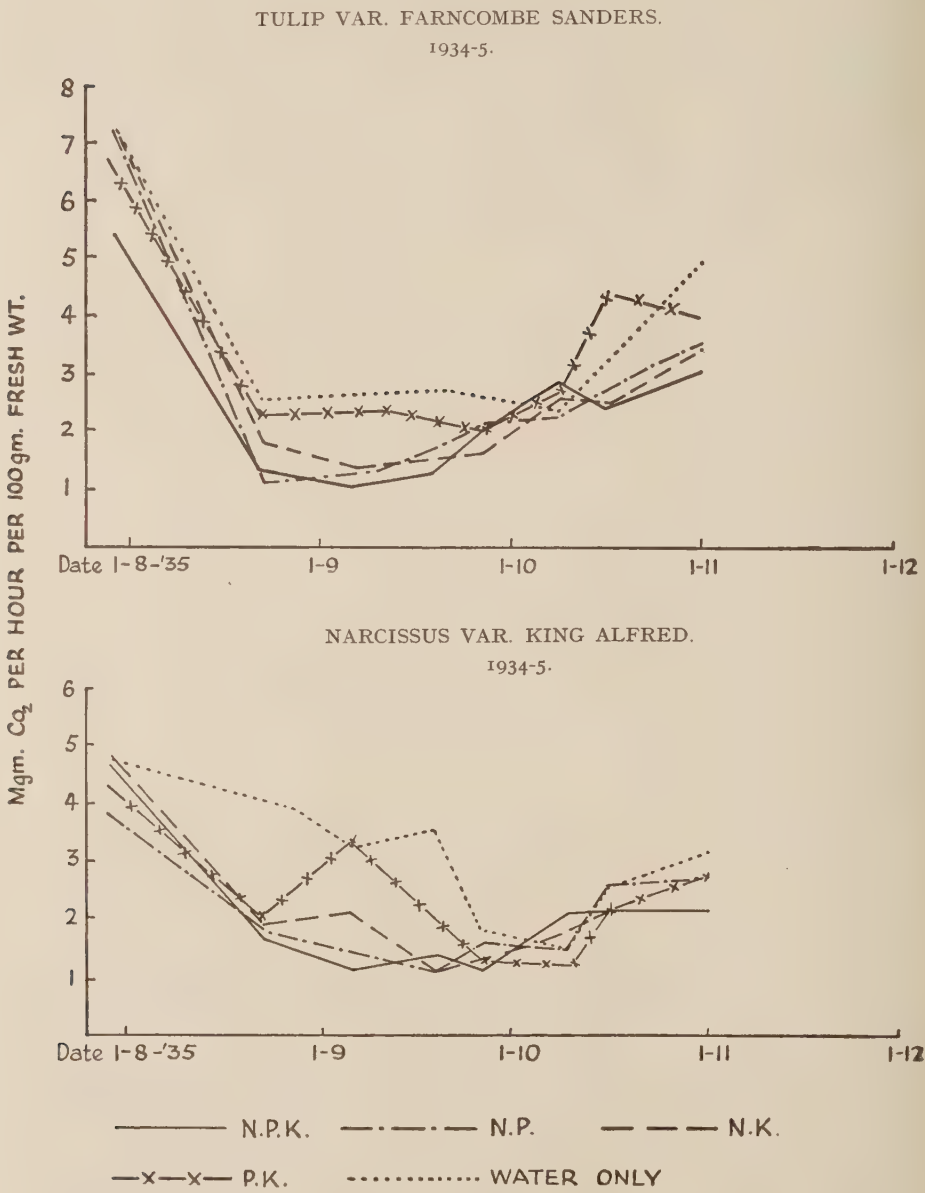
The bulbs were enclosed in glass cylinders which were immersed in a water bath kept at a temperature of 25° C. throughout the duration of the experiment. The air was freed from carbon dioxide by passage through soda lime towers. After passing over the bulbs the air was drawn through Pettenkofer tubes containing baryta water, which precipitated the carbon dioxide as barium carbonate. After aspiration, the baryta water was removed and an aliquot part was titrated with 0·1 N. hydrochloric acid, using phenol-phthalein as indicator. From the differences before and after aspiration, the amount of carbon dioxide given off per hour per 100 gm. fresh weight was calculated.

The apparatus was allowed to run for half an hour (tubes containing water being substituted for those containing baryta water) in order to allow the bulbs to reach the same temperature as the water bath. Six tulip bulbs and three Narcissus bulbs were used for each determination. The same bulbs were used throughout and were weighed before each determination.

Discussion of the results.

The results are shown in Text Fig. 4. It will be noticed that the curves are similar in form for the different bulbs. There is a rapid fall in the respiration rates between the end of July and the end of August, which is followed by a period of low respiration until the middle of September, in tulips, and until the end of September in Narcissus, when the rate of respiration increases again. It will be noticed that the relative rates of respiration for different treatments are the same for both Narcissus and tulip.

Omission of nitrogen, and of all nutrients, has in both cases resulted in a higher rate of respiration. This is contrary to general experience, since the rate of respiration normally increases with nitrogen content where nitrogen is an index of protoplasmic protein. Reference to Tables V and VI shows that bulbs receiving water only, or not receiving nitrogen, had a lower nitrogen content than bulbs under any other treatment. However, in the absence of chemical and morphological data, it is not possible to interpret the results generally or to explain the high rate of respiration of bulbs not receiving nitrogen.



TEXT FIG. 4.
Effect of treatments on rate of respiration of Narcissus and tulip bulbs.

GENERAL DISCUSSION.

In attempting to interpret the results it must be borne in mind that the experimental conditions were very different from those which occur in the field. Whereas under field conditions the roots are in contact with a more dilute, but continuous supply of nutrient solution, in the sand cultures the supply was intermittent, and at the time of application more concentrated. Also the so-called " complete nutrient solution ", which contains all the essential elements for growth, and perhaps in the right proportions for the growth of fruit trees for which it was devised, may have been far from ideal for the growth of bulbs. Since there were no data available as to what constituted a good solution for bulbs, the choice of the one used in the experiments was purely arbitrary.

The compartments used in the first experiments were not entirely satisfactory, but after concreting the bases and leaving a small strip un-concreted for drainage, the risk of contamination from the neighbouring compartments was minimized. The bins used in the experiment on potassium deficiency were satisfactory for this type of work. With some plants the use of galvanized iron containers has resulted in zinc poisoning, but in the present experiments no toxic effect was apparent.

The most interesting result was the small effect that the omission of potassium produced on the general appearance of the plants, particularly of tulips. No leaf scorch developed and the leaves appeared to be quite healthy. It may be mentioned that tulips have been grown under similar conditions for four years without developing leaf scorch. However, although the plants that did not receive potassium appeared to be quite normal, omission of potassium caused a reduction in the bulb weight increase of both Narcissus and tulip. This is an important result from the grower's point of view, since bulbs growing under conditions of potassium deficiency might seem from the appearance of the foliage to be healthy, although the rate of increase in bulb weight would be unsatisfactory. Since potassium is connected with carbohydrate metabolism, and the greater part of the bulb consists of carbohydrates, this result is quite normal and in keeping with the results obtained in manurial trials with such crops as sugar beet, mangolds and potatoes.

It is interesting to note that the omission of potassium did not influence the intensity of the flower colour. Hill and Davis (7), working with Chrysanthemums in sand culture, found that the quantity of potassium, and the ratio of potassium to nitrogen, influenced the flower colour considerably. However, the mobility of potassium in the plant must be taken into account, and the fact that the reserve of potassium in the Chrysanthemum, which is propagated from cuttings, is much smaller than in bulbs.

The omission of nitrogen produced the usual symptoms in the foliage, and a considerable reduction in the bulb weight increase. It should be pointed out

that the potassium : nitrogen ratio in the complete nutrient solution was rather high, and had the nitrogen supply been increased, the bulbs not receiving potassium might have behaved differently, since experiments with fruit trees and other crops have shown that increasing the nitrogen supply accentuates the ill-effects caused by a deficiency of potassium.

The omission of phosphorus did not produce striking deficiency symptoms in the foliage during the first season. Before death the leaves developed purplish tints, a symptom associated with phosphorus deficiency in other plants. Omission of phosphorus caused a considerable reduction in the bulb weight increase of the tulips during the second season.

The growth of Narcissus in these experiments was unsatisfactory. It was thought that the high reaction of the nutrient solution was partly responsible for this, since it is known that Narcissi grow better in soil that has a reaction slightly on the acid side of neutrality. The second experiment, in which the pH of the solution was adjusted to various levels by the addition of sulphuric acid, did not show significant differences in bulb weight increase due to pH. However, determinations made on plants in observation pots showed that the reaction of the nutrient solution soon returned to neutrality, so that conclusions cannot be drawn from this experiment as to the effect of pH on the growth of Narcissi.

An interesting point was noticed when the bulbs in the observation pots flowered. The flowers of the plants not receiving potassium did not appear to be so highly scented as those of the plants receiving potassium. However, this point could not be confirmed from the main experiment, since the flowers could not be isolated ; and it is important that flowers of the same age should be compared.

The treatments employed in the experiments produced marked changes in the nitrogen and inorganic contents of the bulb, but had little effect on the carbohydrates. At the time of sampling, the percentage of reducing and total sugars was low. Starch appeared to be the chief storage material. The omission of potassium did not affect the percentage of carbohydrates to any significant extent, and this suggests that the omission of potassium, at least in the early stages, causes a reduction in the amount of tissue formed rather than in the relative proportions of the storage materials. In both Narcissus and tulip the omission of nitrogen, or of all nutrients, reduced the total nitrogen content of the bulb. In all cases the omission of an element resulted in a lower percentage of that element in the bulb. Since the growth of bulbs in a given season depends to a large extent on the inorganic substances absorbed and the food metabolized during the previous season, and since this is reflected in the organic and the nitrogen content of the bulb, it would appear that analysis of the bulbs for nitrogen, phosphorus and potassium would give some indication as to their performance during the next growing season. Standards would be necessary for comparison and these would probably vary between varieties ; but, taking into account the nature

of the plant, it is thought that such information would be of use in determining the quality of an unknown stock of bulbs, provided that other data, such as purity and freedom from disease were known.

The author wishes to express his thanks to Professor R. H. Stoughton, D.Sc., of the University of Reading, under whose direction this work was carried out, for his continued interest and help and for reading through the manuscript.

SUMMARY.

(1) Nutrition experiments on tulips and Narcissi, extending over the period 1934-7, are described, the bulbs being grown in sand and supplied with different nutrient solutions.

(2) The treatments applied were:—complete nutrient solution, solutions omitting nitrogen, phosphorus, and potassium respectively, and water only.

(3) Qualitative and quantative data were obtained relating to general growth characters, flower stem length, flower quality, bulb weight increase, and chemical composition, as well as concerning the rate of respiration of the "dormant" bulbs.

(4) Omission of nitrogen produced typical deficiency symptoms in the foliage and a significant reduction in bulb weight increase. Omission of potassium, although causing a significant reduction in bulb weight increase, did not produce leaf scorch or affect the quality of the flowers.

(5) The growth of the Narcissi in the second year was unsatisfactory.

(6) The treatments had no significant effect on the carbohydrate content of the bulbs during the first year but produced marked changes in their inorganic and nitrogen content.

(7) It is suggested that analysis of the "dormant" bulbs for total nitrogen, phosphorus, and potassium might prove useful in assessing the quality of an unknown stock of bulbs.

REFERENCES.

(1) *Archbold, H. K.* Chemical Studies in the Physiology of Apples. XII. Ann. Bot., 1932, **46**, 407.

(2) *Denny, F. E.* Eliminating the Use of Calcium Carbonate in preparing Plant Tissue for Analysis. Contrib. Boyce Thompson Inst., 1933, **5**, 103.

(3) ———. Improvements in Methods of determining Starch in Plant Tissues. Contrib. Boyce Thompson Inst., 1934, **6**, 129.

(4) *Gardner, F. E.* Composition and Growth Initiation of dormant Bartlett Pear Shoots as influenced by Temperature. Plant Physiol., 1929, **4**, 405.

(5) *Gibson, G. W.* Some Observations on the Manuring of Bulbs. Sci. Hort., 1935, **3**, 174.

(6) *Handley, F. W.* Manuring of Tulips. Rep. on Experiments with Bulbs, Agric. Inst. and Expt. Sta., Kirton, for the Year 1933 (1934), 23.

(7) *Hill, H., Davis, M. B.* and *Johnson, F. B.* Nutritional Studies with Chrysanthemums. Sci. Agric., 1934, **15**, 110.

(8) *Morris, R. L.* A study of the Determination of Potassium as the Perchlorate, and the Separation from Sodium, etc. Analyst., 1920, **45**, 349.

(9) *Peters* and *Van Slyke.* Quantitative Clinical Chemistry, London, 1932. Vol. 2. 872.

(10) *Shaffer, P. A.* and *Hartmann, A. F.* The Iodometric Determination of Copper and its Use in Sugar Analysis. Journ. Biol. Chem., 1920, **45**, 349.

(11) *Smyth, E. S.* Seasonal Cycles of Nitrogenous and Carbohydrate Materials in Fruit Trees. II. Journ. Pom. & Hort. Sci., 1934, **12**, 249.

(12) *Wallace, T.* Technique in Pot Culture for Fruit Plants. Occ. Paper No. 1, Imp. Bur. Fruit Prod. E. Malling, 1933.

(13) *Walton, G. P.* and *Coe, C. M. R.* Determination of Starch Content in the Presence of Interfering Polysaccharides. Journ. Agric. Res., 1923, **28**, 995.

(*Received* 5/5/39.)

PLATE I

FIG. 1.
Experimental compartments.

FIG. 2.
Planting the bulbs. November 1st, 1934.

The tulips are planted towards the outside, and the Narcissi towards the middle, of the double block of compartments. In the second year all the tulips were planted in the left-hand block, and the Narcissi in the right-hand block.

FIG. 3.
Complete nutrient.

FIG. 4.
Water only.

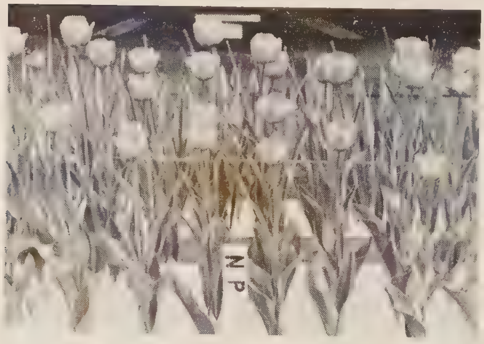


FIG. 5.
Minus potassium.

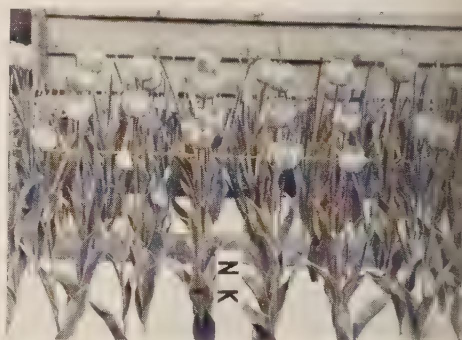


FIG. 6.
Minus phosphorus.

FIG. 7.
Minus nitrogen.

Tulip var. Farncombe Sanders. Photograph taken when the flowers were showing full colour and during the second year of treatment. Note the similarity between the general appearance of plants receiving full nutrient solution (Fig. 3), and plants not receiving potassium (Fig. 5). Note also the edge effects in Figs. 4 and 7.

PLATE III

FIG. 8.

Layout and construction of the trenches for the potassium -pH experiment.

NUTRIENT UPTAKE BY THE TOMATO PLANT

By A. H. LEWIS and F. B. MARMOY
Jealott's Hill Research Station, Imperial Chemical Industries Limited

Introduction.

The course of uptake of nitrogen, phosphate and potash by the tomato plant was described by Owen (1) in 1926. His aim, primarily, was to study the rôle of phosphates in tomato culture, since very little response to phosphatic fertilizers had been obtained at Cheshunt. He showed that the phosphate requirement of the tomato plant is low. The ratio of the amounts of $N : P_2O_5 : K_2O$ in manured plants yielding 5·5 lb. of fruit was 4·6 : 1 : 9, whilst that for unmanured plants giving less than 3·5 lb. of fruit was 5·0 : 1 : 2·8. The main difference was, thus, in potash.

During the course of experiments at Jealott's Hill to study the effects of various chemicals on the growth of tomato plants, it became necessary to use a water culture method, and, in order to decide on the composition of the culture solution, the course of uptake of twelve elements by the tomato plant was studied. As the results for N, P_2O_5 and K_2O differ somewhat from Owen's, and as data on the rate of uptake of the so-called "minor" elements seem to be lacking, the results are presented and discussed in the present paper. While there is in the literature a considerable amount of information on the uptake by various crops of the main nutrients, N, P_2O_5 and K_2O, there is singularly little information on the rate of uptake of the "minor" elements. To help to remedy this deficiency of information, the rate of uptake of a number of "minor" elements is being studied at Jealott's Hill.

Cultural.

Seed (Bill Hill Beauty) was sown in pans in a mixture of leaf mould, loam and sand on January 24th, 1937. The seedlings were transferred to 3-inch pots containing a mixture of 3 parts leaf mould, 1 part loam and 1 part sand on February 10th, and to 5-inch pots of the same medium on March 3rd. The final transfer to 10-inch pots of the same medium, to which sulphate of potash had been added at the rate of 2 lb. to 1½ cwt. of medium, occurred on April 2nd. The plants were spaced at 18 × 18 inches. The temperature of the glass-house was maintained at 65°F. until the air temperature rose above this level.

Manuring was started on June 7th, when the third truss had set. Each plant received (a) ½ oz. nitrochalk and ½ oz. sulphate of potash on June 7th, June 21st, July 5th, etc., and (b) ½ oz. sulphate of ammonia on June 14th, June 28th, July 12th, etc. In all, six applications of (a) and six of (b) were given,

supplying ·068 lb. (30·6 gm.) nitrogen and ·09 lb. (40·5 gm.) potash per plant. Every third week 1 gallon of liquid manure was applied per 10 plants. The liquid manure was prepared by suspending 10 lb. of sheep droppings in a bag in 50 gallons of water, more water being added as required.

Side shoots were nipped out as usual, the top not till mid-August. To avoid complications in chemical analysis, the lower leaves were not stripped off. Some leaves fell off in August.

PLANT SAMPLING.

Out of a batch of 40 plants of even size, plants were selected at random for analysis. The number taken at each sampling varied from 5, in the early stages, to 2, in the final stages. The larger number was necessary in the early stages to give sufficient material for analysis. As soon as the fruit ripened, it was picked, and records were kept of its weight from each plant. It is unlikely that the plants absorbed much nutrient after August 26th, the last date of sampling, since the tops had by then been nipped out, and only a small amount of fruit remained unripe.

RESULTS.

The full analytical results are given in Table I. The roots, which were washed to remove soil, were not analysed in full detail, since their weight was small. Washing does not remove all the adherent soil, and it may lead to some nutrients being leached out. To reduce analytical work, one set of analyses was conducted on a weighted composite sample of ripe fruit. The unripe fruit was analysed in each sample, since the degree of ripeness varied.

Each plant had carried ten trusses when the experiment was stopped on August 26th. The average yield of fresh fruit was about 10 lb. per plant, which corresponds to about 80 tons per acre.

Dry Matter.

The increase in weight of dry matter was slow until towards the end of May, but from then onwards it was very rapid until the end of August. This is in good agreement with the findings of Owen.

PERCENTAGE CHEMICAL COMPOSITON.

(1) *Leaves and stems.*—The percentages of N, P and K in the leaves and stems decreased as the plants increased in weight. This decrease was due to "dilution" by increased photosynthesis and to transfer of nutrients to the fruit. The figures for N and K_2O are about the same as Owen's, but the P_2O_5 figures are higher.

The percentages of Na, S, Fe and Cl in the leaves, and of Na in the stems, increased as the season progressed. Those of Ca, Mg and B in the leaves, and Ca and Fe in the stems remained fairly constant. Those of Mn and Cu in

Date.	Part of Plant.	Dry matter: gm. per plant.	N.	P_2O_5.	CaO.	MgO.	K_2O.	Na_2O.	Fe.	Mn.	Cu.	Cl.	SO_4.	B.
16–4–37	Stem and roots ..	0·67	2·13	0·81	—	—	6·35	—	—	—	—	—	—	—
	Leaves	1·28	3·67	1·05	—	—	5·80	—	—	—	—	—	—	—
	Whole plant ..	1·95	—	—	—	—	—	—	—	—	—	—	—	—
5–5–37	Stem	5·88	2·61	1·60	—	—	9·49	—	—	—	—	—	—	—
	Leaves	9·58	4·27	1·47	—	—	4·60	—	—	—	—	—	—	—
	Roots	1·83	2·83	0·93	—	—	4·05	—	—	—	—	—	—	—
	Whole plant ..	17·29	—	—	—	—	—	—	—	—	—	—	—	—
24–5–37	Stem	19·9	2·24	1·11	1·89	1·22	5·92	0·204	0·0175	0·0045	0·0012	1·66	0·74	—
	Leaves	19·6	4·28	1·11	5·15	1·30	4·30	0·350	0·0340	0·0080	0·0017	1·19	4·20	0·0061
	Unripe fruit ..	5·85	2·92	1·07	—	—	5·24	—	—	—	—	—	—	—
	Roots	4·5	2·67	0·83	—	—	2·94	—	—	—	—	—	—	—
	Whole plant ..	49·85	—	—	—	—	—	—	—	—	—	—	—	—
14–6–37	Stem	38·9	1·54	1·12	2·13	1·07	5·54	0·346	0·0145	0·0029	0·0011	2·68	1·15	0·0026
	Leaves	31·2	3·81	1·12	6·68	1·39	3·97	0·433	0·0296	0·0081	0·0020	2·70	5·73	0·0081
	Unripe fruit ..	42·9	2·56	1·22	0·21	0·38	6·40	0·137	0·0164	0·0016	0·0011	1·10	0·49	0·0021
	Roots	6·2	2·40	0·70	—	—	2·29	—	—	—	—	—	—	—
	Whole plant ..	119·2	—	—	—	—	—	—	—	—	—	—	—	—
25–6–37	Stem	68·3	1·46	0·87	2·03	1·09	3·89	0·365	0·0130	0·0025	0·0012	2·22	0·92	0·0021
	Leaves	48·9	3·95	0·97	5·28	1·40	2·65	0·928	0·0291	0·0079	0·0021	2·48	5·02	0·0085
	Unripe fruit ..	82·9	2·21	1·02	0·20	0·33	5·83	0·102	0·0132	0·0011	0·0009	1·18	0·51	0·0018
	Roots	8·75	2·44	0·62	—	—	1·60	—	—	—	—	—	—	—
	Whole plant ..	208·85	—	—	—	—	—	—	—	—	—	—	—	—
9–7–37	Stem	87·4	1·20	0·69	1·90	1·08	3·26	0·456	0·0110	0·0027	0·0013	2·04	0·68	0·0021
	Leaves	72·3	2·87	0·83	6·79	1·44	2·78	0·765	0·0388	0·0082	0·0016	2·51	5·85	0·0073
	Ripe fruit ..	32·3	2·47	0·99	0·35	0·30	5·58	0·170	0·0290	0·0011	0·0014	0·90	0·37	0·0016
	Unripe fruit ..	121·8	2·13	0·81	0·18	0·25	4·57	0·300	0·0190	0·0011	0·0010	0·95	0·19	0·0018
	Roots	9·9	2·21	0·56	—	—	1·92	—	—	—	—	—	—	—
	Whole plant ..	323·7	—	—	—	—	—	—	—	—	—	—	—	—
29–7–37	Stem	110·0	0·88	0·54	2·03	0·92	3·05	0·640	0·0230	0·0023	0·0010	2·08	0·61	0·0021
	Leaves	78·0	2·21	0·53	7·04	1·12	3·28	0·550	0·0660	0·0080	0·0012	2·46	5·77	0·0083
	Ripe fruit ..	159·5	2·47	0·99	0·35	0·30	5·58	0·170	0·0290	0·0011	0·0014	0·90	0·37	0·0016
	Unripe fruit ..	76·2	1·55	0·67	0·13	0·23	4·47	0·300	0·0150	0·0009	0·0010	1·05	0·12	0·0014
	Roots	14·0	2·29	0·63	—	—	2·54	—	—	—	—	—	—	—
	Whole plant ..	437·7	—	—	—	—	—	—	—	—	—	—	—	—
26–8–37	Stem	136·9	0·81	0·51	1·35	0·83	3·04	0·670	0·0150	0·0014	0·0006	2·44	0·50	0·0021
	Leaves	79·9	1·34	0·35	6·03	1·37	3·79	0·680	0·0840	0·0053	0·0012	3·26	7·28	0·0134
	Ripe fruit ..	262·8	2·47	0·99	0·35	0·30	5·58	0·170	0·0290	0·0011	0·0014	0·90	0·37	0·0016
	Unripe fruit ..	26·1	1·41	0·73	0·13	0·22	4·35	0·380	0·0220	0·0008	0·0008	1·22	0·21	0·0016
	Roots	16·1	2·33	0·63	—	—	2·76	—	—	—	—	—	—	—
	Whole plant ..	521·8	—	—	—	—	—	—	—	—	—	—	—	

the leaves also remained constant until August, after which they fell off sharply. The elements that did not decrease are those present in relatively small amounts in the fruit.

(2) *Roots.*—There were no very marked changes in the percentages of N, P_2O_5 and K_2O. They all decreased until about the end of June, after which they increased slightly.

(3) *Fruit.*—The fruit is low in Ca, Mg, Na, Mn, Cl, S, Fe and B, compared with the green parts of the plant, i.e. in those elements which do not decrease with age in the green parts. A comparison of the results for ripe fruit with those obtained by other workers is given in Table II.

TABLE II.

Chemical Composition of Dry Matter of Ripe Fruit.

		Jealott's Hill.	Owen (1). (K3, 1925).	Sando (2).	Passerini (3).	Stüber (4).	Remington (5).	McHargue (6).	
								Poor soil + complete nutrients.	Blue grass.
Percentages.	N	2·47	2·45	2·48	—	—	—	2·12	3·01
	P_2O_5	0·99	0·78	1·07	—	—	—	0·22	0·73
	K_2O	5·58	4·98	5·42	—	—	—	3·21	5·32
	CaO	0·35	—	—	0·143	0·26	—	0·11	0·47
	MgO	0·30	—	—	0·315	0·42	—	0·18	0·21
	Na_2O	0·17	—	—	0·616	0·26	—	0·70	1·18
	Cl	0·90	—	—	1·99	0·68	—	—	—
	SO_4	0·37	—	—	0·43	0·77	—	—	—
Parts per million.	Fe	290	—	—	290	—	148	150	48
	Mn	11	—	—	—	—	26	52	43
	Cu	14	—	—	—	—	17	6	10
	B	16	—	—	—	—	—	—	—

The figures for N, P_2O_5 and K_2O agree closely with those of Sando (2), which are averages for a large number of samples. Of the other elements, Na and Mn appear to be low in the fruit at Jealott's Hill.

Caution is needed in drawing conclusions regarding the changes that occur during ripening, since the figures for ripe fruit are based on one weighted composite sample. Owen's figures show that there are variations from truss to truss, and in his experiments the third and fourth trusses were highest in percentage nitrogen and mineral matter. His results suggest that there was a decrease during ripening owing to nutrient transfer to the fruit lagging behind the elaboration of organic constituents.

A noticeable feature of the results given in Table I is the steady drop in percentage nitrogen and mineral matter in the unripe fruit from May to August. It might be argued that this drop was due to deficiency of nutrients, but it is difficult to believe that any serious deficiency could have occurred in a crop

TABLE III.

Amounts of Nutrients in the Plant.

(*Maximum amount of nutrient* = 100.)

Date.	Part of Plant.	N.	P_2O_5.	CaO.	MgO.	K_2O.	Na_2O.	Fe.	Mn.	Cu.	Cl.	SO_4.	B.
16–4–37	Leaves	2·3	2·2	—	—	2·4	—	—	—	—	—	—	—
	Whole plant ..	0·6	0·5	—	—	0·5	—	—	—	—	—	—	—
5–5–37	Leaves	20	24	—	—	15	—	—	—	—	—	—	—
	Stem	14	13	—	—	14	—	—	—	—	—	—	—
	Roots	14	17	—	—	17	—	—	—	—	—	—	—
	Whole plant ..	7	7	—	—	5	—	—	—	—	—	—	—
24–5–37	Leaves	40	36	18	23	28	13	10	26	25	9	14	11
	Stem	40	31	17	21	29	5	14	36	18	10	22	?
	Roots	32	37	—	—	30	—	—	—	—	—	—	—
	Whole plant ..	17	14	17	16	11	6	6	22	9	7	13	?
14–6–37	Leaves	58	58	38	40	41	24	14	40	50	32	31	23
	Stem	55	62	24	37	52	15	22	44	36	31	66	35
	Roots	43	43	—	—	32	—	—	—	—	—	—	—
	Whole plant ..	33	35	32	33	27	16	14	38	26	27	33	25
25–6–37	Leaves	94	79	47	63	43	82	21	63	83	47	42	39
	Stem	90	84	62	65	64	27	36	68	73	45	92	48
	Roots	57	54	—	—	32	—	—	—	—	—	—	—
	Whole plant ..	53	51	49	55	38	39	20	58	46	43	47	40
9–7–37	Leaves	100	100	89	95	66	100	41	95	100	70	73	50
	Stem	95	86	74	83	68	44	38	96	100	53	88	62
	Roots	58	55	—	—	43	—	—	—	—	—	—	—
	Whole plant ..	72	66	82	77	53	68	41	90	70	59	69	55
29–7–37	Leaves	84	68	100	80	85	78	76	100	75	74	77	61
	Stem	87	84	100	89	81	77	100	100	100	69	99	79
	Roots	87	87	—	—	80	—	—	—	—	—	—	—
	Whole plant ..	86	82	100	83	79	81	78	100	88	75	78	70
26–8–37	Leaves	52	47	88	100	100	98	100	68	83	100	100	100
	Stem	100	100	83	100	100	100	84	76	73	100	100	100
	Roots	100	100	—	—	100	—	—	—	—	—	—	—
	Whole plant ..	100	100	91	100	100	100	100	82	100	100	100	100

Whole plant includes ripe and unripe fruit.

yielding 10 lb. of fruit per plant. The results for ripe fruit are for analyses of a weighted composite sample. Since 90% of the ripe fruit was picked on July 29th and August 26th, it is obvious that the results were very little influenced by the fruit picked on July 9th. It is, therefore, clear that during August the percentage of nitrogen and mineral matter in the ripe fruit was higher than that in the unripe fruit. This is in disagreement with Owen's finding.

Nutrient Uptake.

A slow rate of uptake of nutrients in the early stages was followed by a period of very rapid uptake during June and July, after which the rate of uptake declined (Table III). The periods of maximum rate of uptake for the various elements were:—

May 24th — July 29th — K_2O and P_2O_5*.
June 14th — June 25th — Cl* and B*.
June 14th — July 9th — N, CaO, MgO, Na_2O, Mn and Cu.
June 25th — July 9th — SO_4*.
June 25th — July 29th — Fe.

The nutrients marked * showed less definite maxima than the others. It will be seen that the period of maximum uptake of N was rather more restricted than that for P_2O_5 and K_2O.

The weights of nutrients in the whole plant are compared with Owen's figures in Table IV. His results for plot K2, which had not been manured for many years, show clearly the effect of lack of potash on yield. A very noticeable feature of the crop on the unmanured K2 plot was the high dry matter content of the green parts of the plant (14·8% compared with 9·5% in K3).

Table IV.

	Gm. nutrient in one plant.			Dry weight, gm.		Remarks.
	N.	P_2O_5.	K_2O.	Green parts.	Fruit.	
Jealott's Hill manured ..	9·4	3·9	23·4	217	289	Over 90% first quality fruit.
Owen M manured ..	9·3	2·2	19·8	172	97	
Owen K3 manured ..	9·3	2·0	18·2	143	149	94% first quality fruit.
Owen K2 unmanured ..	4·9	1·0	2·8	82	74	43% first quality fruit. 43% blotchy.

The yields of fruit at Jealott's Hill were two to three times greater than those from Owen's manured plots. The plants were higher in percentage P_2O_5 content than his, but it would be dangerous to conclude that the higher yields were due to a higher P_2O_5 content, since so many other factors (season, soil, manuring, variety, etc.) may be concerned. As Owen points out, an average yield of 5·5 lb. of fruit per plant (plot K3) is very satisfactory for a glasshouse that has been in regular use for twelve years.

Manuring.

While it is usual to manure and fertilize the tomato crop liberally, it may not generally be realized that a fairly good crop removes about 300 lb. N, 125 lb. P_2O_5 and 600-700 lb. K_2O per acre.

From Table V it will be seen that the ratio of $N:P_2O_5:K_2O$ was fairly constant throughout the life of the crop. This suggests that the supply of manure might be constant in composition but should, of course, be varied in amount according to the stage of growth. In this crop and in Owen's, the ratio of $N:K_2O$ was about 1:2, and it can be concluded that manuring should supply N and K_2O in approximately this ratio. The results indicate a P_2O_5 requirement twice as high as Owen's. In practice it would probably be safer to base manuring on the larger amount of P_2O_5, since the extra amount will do no harm, and may be beneficial.

TABLE V.

Ratios of amounts of nutrients in whole plants.

Jealott's Hill 1938 (i). Planted April 2nd in pots.					Owen M 1926 (ii). Planted March 5th in beds.				
Date.	No. of trusses with fruit set.	N.	P_2O_5.	K_2O.	Date.	No. of trusses with fruit set.	N.	P_2O_5.	K_2O.
April 16th	—	3·4	1	6·5	April 5th	0	4·8	1	10·5
May 5th	1	2·4	1	4·3	May 5th	0	5·0	1	10·1
May 24th	2	2·9	1	4·6	June 5th	2	4·8	1	10·2
June 14th	3	2·2	1	4·7	July 5th	3	4·3	1	9·4
June 25th	4	2·5	1	4·6	August 5th	6	4·3	1	8·3
July 9th	6	2·6	1	4·8	Sept. 5th	6	4·1	1	7·6
July 29th	8	2·6	1	5·8	October 5th	8	4·1	1	8·8
Aug. 26th	10	2·4	1	6·0					

(i) Roots included. (ii) Roots not included.

It is customary to supply in the form of inorganic or organic fertilizers a good deal of the nutrients needed by the tomato crop. It is generally accepted that about 40-50% of the N and K_2O and 20% of the P_2O_5 in fertilizers are absorbed by crops. The ratio of $N:P_2O_5:K_2O$ in the crop is about $2\frac{1}{2}:1:5$, so

that, assuming the above recoveries of nutrients in the crop, a balanced fertilizer would have an $N:P_2O_5:K_2O$ ratio of about 1:1:2. Sometimes rather more K_2O may be needed in the early stages of growth and in dull weather to prevent soft growth, while rather more N may be given in the later stages, but no great departure from an $N:K_2O$ ratio of 1 to 2 seems warranted. It may also be necessary to make slight adjustments on certain soils, but it must be remembered that the amount of nutrients supplied by the soil is small compared with that normally applied in the form of dung and fertilizers. In Jersey, very good results have been obtained by using a fertilizer having a ratio of 1:1:2, both as a basal dressing and for top-dressing.

The above is not meant to imply that bulky organic manures are not needed, since the opposite is clearly the case. The main function of organic manure is to keep the soil in good physical condition, and Bewley (7) states that excellent results have been obtained where the usual dressings of horse manure have been wholly or partly replaced by straw. Nevertheless, when dung is applied, account must be taken of its nutrient content. The strawy type of horse manure favoured for tomatoes probably does not contain more than 0·4% N, 0·25% P_2O_5 and 0·5% K_2O, of which not more than about 20% becomes available in the first season. Horse manure is, thus, unbalanced for tomatoes, being too low in K_2O. Cow dung is similarly unbalanced. Hence, any basal fertilizer dressing should supply a relatively large amount of potash.

It is very unlikely that a deficiency of any "minor" element will limit yields of tomatoes in this country. Not only do most soils contain adequate reserves of such elements, but the generous applications of dung and fertilizers supply relatively large amounts of Mn, B, S, Cl, etc.

SUMMARY.

The course of uptake of twelve elements by the tomato crop has been studied. The relative proportions of nutrients in the crop is tolerably constant throughout its whole life. The rate of nutrient uptake follows the rate of dry matter production fairly closely, i.e. nutrient uptake is slow in the early stages, rises to a maximum in June to July, and then declines.

The results suggest that a nutrient supply of more or less constant composition ($N:P_2O_5:K_2O = 1:1:2$ approximately) might be used, the amount applied being varied according to the stage and rate of growth.

ACKOWLEDGMENTS.

Thanks are due to Mr. M. Thruston for assistance in analytical work, and to Imperial Chemical Industries Ltd. for permission to publish this paper.

REFERENCES.

(1) *Owen, O.* The Analysis of Tomato Plants. Part I. Journ. Agric. Sci., 1929, **19**, 413.

(2) *Sando, C. E.* The Process of Ripening in the Tomato, considered especially from the Commercial Standpoint. U.S.D.A. Bull. 859, 1920.

(3) *Passerini, N.* Sulla Composizione chemica del frutto pomodoro. (Solanum lycopersicum.) Staz. Sper. Agr. Ital., 1890, **18**, 545.

(4) *Stüber, W.* Über die Zusammensetzung der Tomate und des Tomatensaftes. Ztschr. Untersuch. Nahr.-u. Genussmtl., 1906, **11**, 578.

(5) *Remington, R. E.* and *Shiver, H. E.* Iron, Copper and Manganese content of Some Common Vegetable Foods. J. Assoc. Off. Agric. Chem. 1930, **13**, 129.

(6) *McHargue, J. S.* and *Calfee, R. H.* The Necessity of Minor Elements for the Growth of Tomatoes in a Poor Soil. J. Amer. Soc. Agron., 1937, **29**, 385.

(7) *Bewley, W. F.* Tomatoes: Cultivation, Diseases and Pests. Min. Agric. Bull. 77, 1936.

(*Received* 6/5/39.)

PHYSIOLOGICAL BREAKDOWN IN STORED MONARCH PLUMS

By W. HUGH SMITH
Ditton Laboratory, East Malling, Kent

It is now well known that in stored plums physiological breakdown is met with after protracted exposure to low temperatures. Kidd and West (1) first reported the occurrence of internal breakdown in English plums. Smith (2) studied the effect of maturity at picking time and that of storage temperature on the progress of physiological breakdown in the variety Victoria. Rees Davies (3), in South Africa, has made a comprehensive study of the problem of physiological breakdown in a range of varieties, and more recently certain theoretical considerations have been brought forward by Van der Plank and Rees Davies (4) in an attempt to interpret the phenomena.

The experiments reported in this paper aimed at providing information as to the behaviour of a European variety of plum, grown under English conditions, when subjected to a considerable range of storage temperatures. For this purpose the variety Monarch was chosen, since it was known to be extremely susceptible to physiological breakdown.

Material and Method.

The plums for the experiment were obtained from a local orchard. They were picked on August 26th, 1938, from 38 trees of somewhat varied size and bearing, and were stored on the evening of the same day. Since the trees were completely stripped of fruit at the one picking it was possible to obtain plums of a large range of maturity. They were therefore sorted into two groups:—

A. More mature fruit ; from $\frac{3}{4}$ to full purple colour ; firm.

B. Less mature fruit ; from $\frac{1}{4}$ to $\frac{3}{4}$ purple colour (remaining area green) ; hard.*

Plums with a transverse diameter of less than about 4 cm. were eliminated, as were also those showing rots or severe injury due to hail or insect wounds.

The graded fruit was sampled in the usual way the samples being made up of 50-60 fruits, each sample containing as far as possible an equal number of fruits from each tree.

Measurements of respiration on parallel samples of the plums revealed that the fruit was "pre-climacteric" at the time of picking.

* The two groups will be referred to by their letters throughout the paper.

CONDITIONS OF STORAGE.

The plums were stored on wooden trays lined with paper, at the following constant temperatures:—

65°F. (18·3°C.), 50°F. (10°C.), 45°F. (7·2°C.), 40°F. (4·4°C.), 37°F. (2·8°C.), 34°F. (1·1°C.), and 31°F. (−0·6°C.).

Samples were removed from store at intervals of 7 days and cut open for examination. A duplicate sample was usually placed at 65°F. for observation during ripening.

THE EFFECT OF TEMPERATURE AND DURATION OF STORAGE PERIOD.

In Table I is shown the total physiological breakdown occurring at each examination expressed as a percentage of the unrotted plums. The difficulty of detecting breakdown in plums affected by fungus rots precluded calculation on the basis of the total sample.†

TABLE I.

Total Physiological Breakdown in Monarch Plums.

Number of days in store.	Temperature of Storage ° F.						
	31	34	37	40	45	50	65
	Group A (more mature). Physiological Breakdown (%).						
7	0	0	0	0	0	—	0
14	0	0	5	5·5	28	28	—
21	15	7	31·5	40·5	88	75	(96)*
29	56	40	73	78	88	75	—
35	81	77	94	98	96	—	—
42	96	95	—	100	—	—	—
49	100	98	—	—	—	—	—
	Group B (less mature). Physiological Breakdown (%).						
7	0	0	0	0	0	—	—
14	0	0	0	0	0	0	0
21	11	3·5	10	25·5	58	44	—
29	32	5	13	25·5	64	54	—
35	70	27	42	51	84	—	—
42	92	56	66	80	90	—	—
49	98	82	92	95·5	100	—	—
56	98	89	98	100	92	—	—
64	100	94	100	—	—	—	—

* A pseudo-jellied state subsequent to the normal juicy state.

Storage at 65°F.

At 65°F. about 96 per cent. of the plums of group A ripened in 7 days, and a similar percentage of group B took 13 days to ripen. In each lot the ripened plums were normal, although those of group B were rather lacking in flavour and in the typical ripe-plum odour.

† Only after prolonged storage at the higher temperatures did rotting due to fungi assume significant proportions.

Storage at 50°F.

After 14 days at 50°F., 28 per cent. of the plums of group A had jellied,* the remainder being still unripe. After 21 days, 75 per cent. had jellied, the remainder being juicy and normally ripe. Of the B group 44 per cent. were jellied on the 21st day of storage, the remainder being mainly unripe. After 29 days, 54 per cent. had jellied, the remainder being normally juicy and ripe. It was thus evident that only some of the plums were capable of ripening normally at this temperature and that this proportion was relatively higher in the plums of group B than in those of group A. It was noted that the plums of group B which attained a juicy stage of ripeness had a relatively weak ripe-plum odour and were lacking in flavour.

Storage at 45°F.

Ripening at 45°F. was abnormal, jellying of the flesh with or without brown discoloration affecting 96 per cent. of the plums of group A by the 35th day and 100 per cent. of group B by the 49th day.

Storage at 40°F. and 37°F.

At these temperatures jellying of the flesh occurred with or without brown discoloration affecting all the plums in group A by the 42nd day and in group B by the 56th day. Ripening was therefore completely abnormal.

Storage at 34°F. and 31°F.

No jellying occurred during storage at these temperatures, but the flesh of the plums became severely browned before appreciable softening had taken place. By the 42nd day, 96 per cent. of the plums of group A at 31°F. were discoloured, and 92 per cent. of group B.

Consideration of the above results showed that there must be a critical temperature between 50°F. and 65°F. below which some of the plums would not ripen, the proportion increasing rapidly the lower the temperature. In place of the changes which occurred when ripening was normal—namely, softening of the flesh accompanied by the production of copious juice, and the development of characteristic flavour and odour—certain abnormal changes occurred, which may now be described.

Jellying of the Flesh. In plums disposed to jellying, softening proceeded, but instead of yielding juice, the flesh became relatively dry and mealy. This condition may be limited to a portion of the flesh which becomes contrasted with the remainder by its dark, injected, appearance. In advance stages of jellying, a ring of whitish spongy tissue was frequently found around the stone. Examination revealed the presence of numerous gas bubbles in this spongy tissue. It is interesting to note that this condition was found during storage only in plums stored at 37°F. or above that temperature.

* A full description of the jellied condition is given below.

Internal Browning. Internal browning was the characteristic disorder in plums stored at 31° F. and 34° F. This term is used to describe a condition of the flesh in which a brown discoloration spread through the tissues. In the early stages it appeared as flecks of brown, radiating outwards from the stone. Later, the vascular strands became discoloured, and then browning became general. Frequently a ring of comparatively sound tissue could be found beneath the skin. Browning also occurred in the plums kept at the higher temperatures, but it then invariably accompanied a soft jellied condition of the flesh of the fruit, and the frequency with which it occurred was less than at the lower temperatures.

In Fig. 1 are reproduced curves showing the percentage total physiological breakdown (jellying + internal browning) in relation to temperature of storage. The following are the main points of interest:—

Total physiological breakdown made its appearance in an increasing percentage of plums throughout the period of storage. Eventually all plums showed breakdown, irrespective of temperature, when stored at or below 45°F. With the more mature plums of group A, physiological breakdown had appeared at and above temperatures of 37°F. by the 14th day of storage. No breakdown was evident at any temperature on the 7th day.

With the less mature plums of group B, no breakdown was found on the 14th day, but on the 21st day it occurred at all temperatures.

The percentage of plums with breakdown increased more rapidly at 45°F. than at any other temperature. The least rapid increase occurred at 34°F., at which temperature the smallest amount of breakdown was always to be found at any examination. At 31°F., again, there was a rapid acceleration in the appearance of breakdown comparable to that at 45°F., though in this case taking the form of internal browning instead of jellying. It will be seen that all the curves have a very characteristic sigmoid form.

After-Storage Ripening at 65°F. and the Occurrence of Physiological Breakdown.

Immediate examination of the plums on withdrawal from storage gives no reliable indication of the amount and intensity of breakdown which will ultimately develop at ripening temperatures. The precaution was therefore taken to set aside a sample on each examination date and to keep it for a period of 6-8 days at 65°F. before cutting the fruits.

The advance of physiological breakdown in plums of group B at 65°F., *after* storage at low temperatures for 14, 21 and 29 days, is illustrated in Fig. 2 where curves are drawn through the values for percentage breakdown both immediately on removal from storage and after 8, 6 and 7 days respectively, at 65°F.

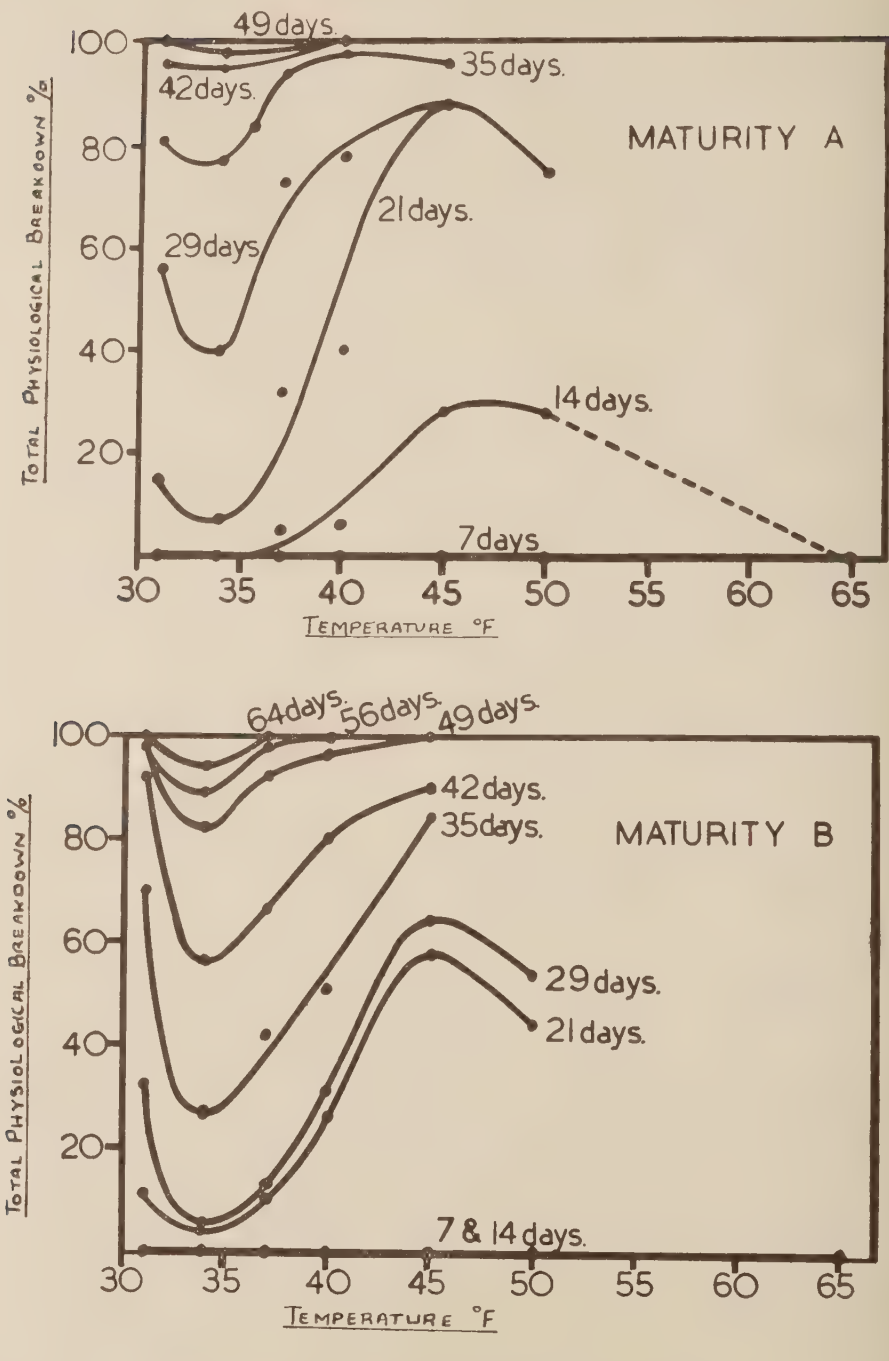


Fig I Physiological Breakdown of Monarch Plums in relation to Temperature & Duration of Storage

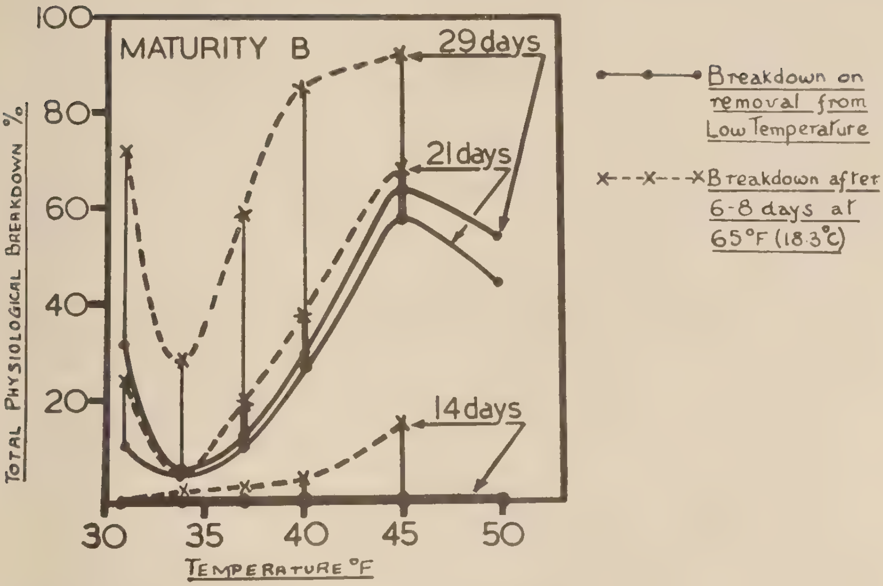


Fig 2. The Development of Physiological Breakdown in Monarch Plums at 65°F (18·3°C) after storage at Low Temperatures.

Whereas after 14 days no breakdown was evident in the plums immediately after removal from storage at any temperature, subsequently some breakdown developed after 8 days at 65°F., a maximum of 15 per cent. being found in those from 45°F.

A slight increase of breakdown at 65°F. was observed after storage for 21 days at all temperatures, and a greater increase after 29 days. The curves for breakdown after exposure to room temperature are in all cases similar in form to those for breakdown during storage. In plums of group A, physiological breakdown appeared after only 4 days at 31°F., 37°F. and 45°F.; when kept for a further period of 7 days at 45°F., a maximum of 13·5 per cent. was found after storage at 45°F.

DISCUSSION.

From a consideration of the curves in Fig. 1 it is clear that the effect of a greater degree of maturity at picking was to advance in time the first appearance and maximum development of physiological breakdown. The characteristic forms of the curves show that in no way were the relative amounts of breakdown as between temperatures at the successive examinations disturbed by differences of maturity.

From the shapes of the curves it is evident that the maximum amount of breakdown after 14-21 days of storage occurred at an intermediate temperature. After longer periods, higher maxima occurred at progressively lower temperatures.

Van der Plank and Rees Davies (4) have attempted to explain the occurrence in South African fruits of the maximal amount of breakdown at intermediate temperatures, and the delayed maximum at lower temperatures, in the following way:—

They introduce the concept of an "equilibrium factor" which maintains the fruit in a balanced state of metabolism at higher temperatures but rapidly upsets the balance at low temperatures. The lower the temperature of storage the greater the disposition towards injury. But another, and opposing factor, a "kinetic factor", is introduced to explain the fact that, while a greater amount of injury is sustained at the lower temperatures, it becomes manifest very much later than the smaller amount of injury at the higher temperatures. This factor is supposed to govern, in accordance with thermo-chemical laws, the rate of progress of the disorder arising out of the initial lack of balance. The lower the temperature, therefore, the greater the upset to the metabolic balance; but the slower the development of manifest injury. The ultimate maximum amount of breakdown at any given temperature is taken to be an approximate measure of "primary susceptibility", and is determined shortly after cooling to that temperature.

Considering the curves in Fig. 1 it is evident that according to this conception the primary susceptibility of this population of plums may be considered to be 100 per cent. at 45°F. and at all temperatures below 45°F. It is less than 100 per cent. at temperatures above 45°F. and falls to nil at some temperature between 50°F. and 65°F.

It is difficult to see how the characteristic trough, which occurs consistently at 34°F. in all the curves, can be explained in the light of the "kinetic factor". According to this interpretation it would be necessary to have a smooth and regular transition between the values at 45°F. and 31°F.

Further, there seems to be no justification for overlooking the symptomatic distinctions between "jellying" and "internal browning". Although at intermediate temperatures it is difficult to draw a clear-cut line of distinction, it should not be overlooked that two types of injury, with distinct causal relations, may be involved.

It is suggested therefore that since at 34°F. and below, no jellying was observed to occur, and at 45°F. and above, no internal browning, the Monarch plum is actually susceptible to two separate types of injury. At 45°F. and above, the plums are susceptible only to the jellying type, the degree of susceptibility

falling to nil with rise of temperature.* At 34°F. and below, they are susceptible only to the internal browning type, the degree of susceptibility increasing rapidly with lowering of temperature.

Between 34°F. and 45°F. plums may be susceptible to both types of disorder, which may affect one and the same plum or different plums in a given population. Susceptibility to browning within these limits of temperature will, however, *decrease* with rise of temperature, while susceptibility to jellying will *increase* with rise of temperature. The characteristic forms of the resultant series of curves reproduced in Fig. 1 will then be considered to be an expression of the susceptibility of this particular crop of Monarch plums to two separate, but interacting, factors, producing types of disorder which are symptomatically distinguishable.

It is proposed to make a further examination of the factors determining the susceptibility of this plum to each type of disorder.

SUMMARY.

The effect of storage temperature, duration of storage and degree of maturity at picking, on physiological breakdown in a crop of Monarch plums is described.

The effect of increased maturity at picking was to advance in time the first appearance and maximum development of physiological breakdown at each temperature.

In the early stages, the maximum percentage of plums affected was found at intermediate temperatures. At lower temperatures, while the amount of breakdown ultimately reached 100 per cent., the maximum was reached very much later.

The minimum percentage of breakdown was always found to occur at 34°F., a rapid rise in the amount of breakdown being found both above and below this temperature.

It is suggested that total physiological breakdown resolves itself into two distinct types of injury, distinguishable symptomatically as " internal browning ", and " jellying ", with probably different causal relations.

REFERENCES.

(1) *Kidd, F.* and *West, C.* Report of the Food Investigation Board for the year 1923, 40.

(2) *Smith, W. H.* The Fruit Grower, February 4th, 1937, 161.

(3) *Rees Davies.* Reports of the Low Temperature Research Laboratory, Capetown, for the years 1933, 1934-5 and 1935-6.

(4) *Van der Plank, J. E.* and *Rees Davies.* Temperature-Cold Injury Curves of Fruit. Journ. Pom. & Hort. Sci., 1937, **15**, 226.

* It was noted that plums which ripened normally at 65° F. subsequently at that temperature passed into a state somewhat similar to jellying. (See Table I.) It might appear that at lower temperatures the " juice " stage was, so to speak, " short-circuited " in the plums which were susceptible to jellying.

(*Received* 11/5/39.)

BOOK REVIEW

COMMERCIAL FRUIT TREE SPRAYING: METHODS AND COSTS. By J. Turnbull. (Bulletin No. 5. Ministry of Agriculture and Fisheries, Fourth Edition, 1939, pp. 76 + vi. 1s. 6d.)

Pest and disease control is nowadays an item of considerable expense in fruit production of which the greater part is incurred by spraying and dusting operations. Mr. Turnbull has, for years past, collected first-hand information concerning costs, and this is incorporated in the present edition of *Commercial Fruit Tree Spraying and what it Costs*, the title of previous editions.

The Bulletin opens with general considerations of spray materials, programmes and damage, with particular reference to the quantities of spray generally applied in commercial practice. Then follow sections on recording, on the performances of different types of spray nozzles and on the various methods of conveying the spray fluid to the nozzles. The Bulletin closes with a brief reference to dusting and atomization methods.

The scope of this Bulletin does not greatly exceed that of previous editions, and the reader may be puzzled by the change of title. The inclusion of "methods" in the new title might lead him to expect some description of the various spray appliances now available, and of suitable lay-outs of mixing tanks, pumps and pipes; he might even expect to find some discussion of the mechanical merits and demerits of different pumps and accessory apparatus, or practical hints on the modes of application. But Mr. Turnbull, presumably assuming that the reader is acquainted with these matters, proceeds at once to the discussion of field performances relative to output and labour requirements.

A second point for comment is, that the author confines his observations (with three exceptions) to trials in which he personally collaborated and is inclined to overlook the results of other investigators. For example, he ascribes the development in spraying methods during the last seven years to the results of demonstrations carried out near Maidstone in 1932 and 1933. But these developments were already obvious in American orchard practice and in the experimental work of Marsh and Maynard at the Long Ashton Research Station. It is also difficult to understand why the author was not acquainted with the investigations then proceeding at Wye on protective sprays suitable for application in heavy amount. Actually, Mr. Turnbull mentions the Long Ashton work on page 10 when his observations seem to afford an example of a tendency to ignore facts that conflict with his own hypothesis. In this case, the author's purpose is to show that protective fungicides are more effective in controlling apple Scab when applied in copious amount than when applied "as a fine misty spray". The reason for the use of large quantities of spray fluid in the Long Ashton work was, however, to accelerate application so that two pre-blossom sprays could be used. The freedom from Scab obtained was attributed by Marsh and Maynard not only to thoroughness of application but also to the additional protection afforded by the extra early application. Throughout pages 8-11 the argument that the poor commercial Scab control generally obtained before 1932 was due to inferior methods of application is unduly weakened by ignoring the modification of dates of application which accompanied the change to higher spray pressures and larger nozzle outputs.

The text itself leaves the impression that Mr. Turnbull has become so familiar with certain expressions and terms, that he assumes that this familiarity is shared by his readers. Thus, most of the tables are ill-provided with self-explanatory headings; that on page 18, for example, is headed "No" (presumably of the trial), "Pressure (lb.)" (probably per sq. inch), "Disc" (with no indication of the meaning of "N" and "H", while the numbers there quoted presumably define the diameter of the aperture in 64ths of an inch). The author's statement that, from the contents of this table, "it will be seen at once that . . . the whole basis of previous ideas on spraying would disappear", is too optimistic.

Such difficulties are probably the result of drastic compression. It is to be hoped that the author will be able, in further editions, to enlarge the Bulletin and not only explain adequately the matter he now presents but enlarge the scope of this subject matter to conform to the title. At the same time minor pitfalls such as the implications that Capsids trouble the apple-grower in U.S.A. (page 3), that correct spraying will kill maggots in the core of the apple (page 28) and that delays due to bad weather seldom occur if the spraying plant is oversize (page 34) might be avoided.

The purpose of the above suggestions will be misunderstood if they convey the impression that the information given by Mr. Turnbull is inaccurate or obscure. The Bulletin is full of most useful data and of helpful hints; and, although much of the present review is admittedly critical, the points raised are of minor significance in comparison with the great merits of Mr. Turnbull's work.

Hubert Martin.

EDITORIAL NOTICE

Owing to the abnormal conditions arising from the exigencies of war the Publication Committee has been obliged to give serious consideration to the question of the continued publication of the Journal of Pomology and Horticultural Science.

The present number completes Volume XVII and conforms to the usual standards in respect of contents, size and general make up. It has now been decided to continue publication during 1940, although some modification of the standards in regard to number of pages, quality of paper, etc., may become imperative, and dates of issue may possibly be somewhat irregular. For the present, at any rate, the subscription rate will remain unaltered, viz. 25s. for the Volume (Four Numbers) post free ; single Numbers 7s. 6d. each. Subscriptions are due in January 1940 and should be sent to Messrs. Headley Brothers, 109 Kingsway, London, W.C.2.

Subscribers will greatly facilitate the Committee's task by forwarding the amounts due as promptly as possible.

In view of the ever increasing costs of production contributors of papers are particularly urged to make their MSS as brief as is compatible with accuracy and clarity. Tabular matter should be reduced to a minimum and only really essential illustrations should be included.

In the interests of Horticultural Science it is confidently hoped that all concerned will co-operate with the Committee in ensuring that the results of research shall still find adequate publicity even in times of stress and difficulty such as those at present prevailing.

B.T.P.B.
R.G.H.
G.H.P.

EDWARD A. BUNYARD, F.L.S.

AN APPRECIATION

Those who are associated in running the JOURNAL OF POMOLOGY AND HORTICULTURAL SCIENCE are loath to let this number appear without placing on permanent record some sketch, however slight, of its founder, Edward Bunyard, whose tragic death occurred in November. He it was who started the JOURNAL OF POMOLOGY in 1919, assuming full responsibility for running it for two years. When it was adopted as the official organ of the Long Ashton and East Malling Research Stations, and deliberately extended its title to embrace a wider field of horticultural science, Bunyard continued to serve as Editor for a year and remained an active member of the Publication Committee throughout.

Bunyard's contribution to pomology will be remembered chiefly for his rare combination of systematic historical research with accurate observation of the growing plant. That he loved old books for their own sake is implicit in all his published work. "This article," he says on one occasion, "presents the fruits of a hurried search in Italian bookshops and street barrows, a pursuit demanding some patience and an entire disregard for dust."

At the same time he was no mere bookworm, being adept at selecting his quotations from old books either to confirm some experimental finding or to suggest some new investigation. His "Guide to the Literature of Pomology", which appeared in the Journal of the Royal Horticultural Society in 1915, is a good example of this, and his "History of the Paradise Stocks", which appeared in the first volume of this Journal, shows a model application of the historical and literary methods to systematic pomology.

An important feature of Bunyard's work was his insistence on the need for meticulous accuracy in botanical descriptions, and for making such descriptions from the actual growing plant. "Accurate nomenclature," he writes in "A Winter Study of Fruit Trees", "can only be achieved by a study of our trees and fruits in all their aspects." He was too scientifically minded to accept blindly the statement of some "old master" of pomology, however distinguished, and his many references to literature are none the less valuable for the criticism of the subject matter which often accompanied them. There are many examples in his published work of his passion for accuracy of detail in botanical description. In the first article he wrote for this Journal he questioned the accuracy of stem length as a guide to the identification of pears; in the introduction to his "Handbook of Hardy Fruits", he made a reasoned appeal for the use of spur leaves in preference to shoot leaves as an aid to uniformity in

EDWARD A. BUNYARD, F.L.S.

description ; and he emphasized the importance of leaf-pose as an additional aid to the recognition of varieties. Some of the best examples of his gift for combining critical historical research with accurate botanical description are to be found in the admirable series of articles on the history and development of the red currant, the raspberry and the strawberry, and in those on the classification of gooseberries and of apples.

That would, however, be a grossly one-sided picture of Bunyard which gave only the impression of a gifted bibliophile with a flair for apposite quotations and a nice eye for botanical detail. No man having George Bunyard for a father could fail to have been brought up in a richly practical atmosphere of fruit growing and tree raising, and Edward Bunyard remained true to this background in the sense that he made the successful growing of the plant the ultimate aim of all his researches into fruit and flowers. A very full knowledge of the practice of horticulture is instinct in his article on the cultivation of cobs and filberts, and in that on fig-growing ; it appears again in his description of fruit growing in Switzerland, published in the second volume of this Journal under the title of "A Pomological Pilgrimage".

His detailed knowledge of cherries, arrived at through long and patient study of the actual trees grown by himself, was well known and much appreciated in Kent ; and Kentish cherry growers, through their Show Committee, paid him the singularly graceful compliment of electing him yearly, for fifteen years, as first choice Judge of their own cherries at their own Show.

In his Introduction to the first volume of the "Handbook of Hardy Fruits", the vade mecum of all who have to attempt the identification of varieties grown in this country, he ventured to express the hope that his work might fill the place formerly occupied by Dr. Hogg's "Fruit Manual" ; and certainly there would seem no one more fitting than Bunyard to carry on the great tradition of pomological systematists.

Sir Daniel Hall, who worked with him for many years on various horticultural committees, writes as follows: "Bunyard was a good talker ; he was widely read, had a flair for words and a great gusto so that he could make you share his enjoyment of an apple or a wine or an old book. In his own field he carried an immense knowledge, both of fruit and flowers and of the literature appertaining to them. It was an exact knowledge too, as could be seen in the minute examination he would give to the settlement of the name of an apple or an old rose. But though Bunyard had spent his life amongst fruit trees and garden plants, though he had a most discerning eye and was a shrewd judge of work in the plantations, I always felt that his interest in horticulture was more aesthetic and literary, than scientific and economic. It is indicative that he introduced no new varieties of fruit, though he rescued Orleans Reinette from an undeserved neglect, and from him you could obtain a few uncommon

vegetables and herbs that he had picked out through his fine taste in cookery. He wrote well ; his ' Anatomy of Dessert ' should have a long life ; even if it is at times a little precious that is only the indulgence of a virtuoso toying with the things he loved. For that is what Bunyard should have been—a gentleman of leisure living in his library and his garden, and cultivating by judicious travel a nice taste in matters of kitchen and cellar, instead of having to do business in a world that was ever growing harder and more insensitive.''

Bunyard's loss will be felt keenly by the horticultural world to which he gave lavishly of his time and knowledge on such bodies as the Joint Fruit Trials Committees and the Council of the Royal Horticultural Society. Quite recently he had most appropriately taken on the care of the Library and the Editorship of the Journal of the Royal Horticultural Society.

His loss in the prime of life and in the midst of his many activities, with much useful work still on hand, inevitably constitutes a severe blow to all who are interested in the science of pomology. This Journal, while mourning the death of its founder, can at least do something to keep active in its pages that spirit of scientific pomology which Edward Bunyard did so much to establish in this country.

THE EFFECTS OF A DEFICIENCY OF CERTAIN ESSENTIAL ELEMENTS ON THE DEVELOPMENT AND YIELD OF CARROTS, ONIONS AND RADISHES GROWN IN SAND CULTURES UNDER GLASS

By R. M. WOODMAN
Horticultural Research Station, Cambridge University

THE experiments described in this communication are part of a general scheme of research which is being carried out with the object of ascertaining what effects are caused by deficiencies of the essential elements for plant nutrition on the growth, appearance, yield and quality of vegetables.

EXPERIMENTAL AND OBSERVATIONAL.

The plants were grown in ordinary, new, unglazed earthenware pots of 9 inch diameter, the outer walls of which were coated with copal varnish to prevent loss of water by evaporation. The drainage holes in the pots remained open. Each pot contained about 13 lb. of a special siliceous sand of the kind used in previous work (4). After placing the sand in the pots it was moistened with the respective solutions mentioned below, and the pots were watered with definite quantities of these solutions at intervals throughout the experiments. The total quantities supplied for each crop are given later.

TABLE I.

Solutions.	Parts per million of Important Elements in the Solutions.							
	N.	P.	K.	Ca.	Mg.	Fe.	S.	Na.
A (control) ..	16·48	5·46	22·44	18·06	5·05	0·50	16·15	35·18
B	*0·41*	5·46	22·44	18·06	5·05	0·50	16·15	*8·78*
C	16·48	*0·27*	22·44	18·06	5·05	0·50	16·15	*27·49*
D	16·48	5·46	*1·12*	18·06	5·05	0·50	*7·41*	35·18
E	16·48	5·46	22·44	*0·90*	5·05	0·50	16·15	35·18
F	16·48	5·46	22·44	18·06	*0·25*	0·50	*9·82*	35·18

The seeds were sown directly in the sand in the pots, thus avoiding transplanting, and ensuring that they germinated in contact with the respective solutions. After germination, the seedlings were reduced to one per pot.

The six solutions employed are set out in Table I which shows the concentrations of the important elements present in them. The salts used in supplying these elements were similar to those employed in a previous experiment with lettuces (4) and were of the Analar brand.

Solution A acted as a control which contained the necessary elements in such proportions as to ensure a plant of good average growth. The five solutions B-F showed a marked deficiency of one element, nitrogen, phosphorus, potassium, calcium, or magnesium, respectively. Divergences from the quantities present in the control are italicized in the Table.

For each of the six solutions employed there was a series of sixteen pots, and these were arranged in a greenhouse in randomized-block fashion. Details concerning prevailing temperatures and other factors affecting growth and development are given later for each of the crop plants concerned.

CARROTS.—The seed, variety Primo, of Watkins and Simpson, was sown on June 12th, 1936. Germination was complete by June 20th, and the seedlings were singled on June 23rd. The harvest was on August 20th, 1936. During the experiment every pot received $15\frac{1}{2}$ litres of its solution, usually on alternate days in quantities of 200, 300 or 500 c.c.

The temperature of the unheated greenhouse ranged from 60-80° F. throughout most of the experiment. Daily averages of hours of sunshine were: 1st week, commencing June 19th, when germination was nearly complete, 9·9; 2nd week, 4·0; 3rd, 4·8; 4th, 4·7; 5th, 4·5; 6th, 6·9; 7th, 2·1; 8th, 3·5; and 9th, ending on the day of harvest, August 20th, 6·8.

The controls (A) had tops of normal green colour without signs of scorch or chlorosis. The roots were generally good, straight and tapering, of a very attractive light salmon-red colour. Deficiency of nitrogen (B) resulted in stunted tops of a lighter green shade than the controls. The plants were normal in shape, but small. The roots were not quite so dark in shade as the control roots. Phosphorus deficiency (C) induced very small plants with tops of a slightly darker green shade than the controls, with a tendency to become yellowish-green and to die off; certain of the tops turned definitely dark bronze in shade. The roots were similar to those of the control carrots.

Potash deficiency (D) resulted in large tops with some leaves as dark as the controls, but others lighter. There was a tendency to variegation, and the older leaves were somewhat chlorotic. The plants exhibited a spreading habit. There was scorch of the older portions of the tops, which were inclined to become limp and scorched in green-brown (1), flaccid patches, and then to wither to a limp (not brittle) state. The roots were nearly equal in size, and were equivalent in colour to those of the controls, but showed a slight tendency to curve, and for lateral rootlets to develop into small fangs.

Deficiency of calcium (E) resulted in moderately large plants with tops of similar green colour to those of the controls, but with some chlorotic leaves and tips of leaves. The chlorosis became less pronounced with age. The roots were normal in general appearance except for a tendency to stumpiness and fanginess. Magnesium deficiency (F) led to large plants of similar green shade

to that of the controls, with a tendency to variegation and chlorosis ; the roots were slightly redder than those of the controls.

ONIONS.—The seed, variety Unwin's Reliance, was sown on September 8th, 1936. Germination was complete by the 14th, and the seedlings were singled on September 16th, 1936. The onions were harvested on August 10th, 1937. During the experiment each pot received 36 litres of its solution, usually in quantities of 300 c.c. every three days.

Till mid-October 1936, the greenhouse was unheated, and temperatures ranged from 50-70° F. ; it was then heated until May 1937, and the temperature was fairly constant at 50-55° F. ; the subsequent variations in the temperature up to harvest were generally from 50-80° F. The average daily hours of sunshine were : period September 14th-30th, 1936, 3·8 ; October, 3·7 ; November, 1·8 ; December, 2·2 ; January 1937, 1·6 ; February, 2·4 ; March, 3·6 ; April, 2·8 ; May, 5·5 ; June, 6·7 ; July, 3·6 ; August 1st-10th, 1937, 7·2.

The controls (A) were normal plants. Deficiency of nitrogen (B) led to much smaller plants with very pale green tops, the oldest leaves of which tended to become chlorotic and to die off, the new ones then carrying on the plant. Phosphate deficiency (C) at first resulted in plants of lighter green shade than the controls but, with the new spring growth, in April 1937, the colour became equivalent to that of the controls. There was a strong tendency for the older leaves to wither back from the top and for sturdy young leaves to carry on vigorous growth, so that the heights of the plants were continually varying in cycles, getting less as the old leaves withered, and then greater as the new ones grew.

With potassium deficiency (D) plants of about the same colour as the controls, but smaller, were obtained. There was a tendency to chlorosis in one or two plants. There was also a strong tendency for the oldest leaves to die back progressively from the tip ; not in the form of a dry withering, as with phosphate deficiency, but as a soft wilt, the top portions becoming a dark greenish-grayish brown colour (1), with a satiny texture, and hanging down limply. The new growth carried on the plant as the old leaves withered back and died. The plants in general had an upright habit of growth not present with any other treatment.

Calcium deficiency (E) resulted in smaller plants lighter green in colour than the controls, though ultimately the colour levelled up. There was a tendency to a floppy habit of growth, with wilted leaves, similar to those of plants suffering from potash deficiency. Deficiency of magnesium (F) led to somewhat similar results.

RADISHES.—The seed, variety Red Turnip Radish, extra early Short Top Forcing, of Watkins and Simpson, was sown on July 3rd, 1936. Germination

was complete by the 6th, and the seedlings were singled on the 8th. The harvest was on July 23rd, 1936. During the experiment every pot received 4,200 c.c. of its solution, usually in quantities of 200 c.c. a day.

During this experiment the greenhouse was unheated, and the temperature ranged from 60-85° F. The daily averages of hours of sunshine for three-day periods were: 1st period, commencing July 6th, 4·4; 2nd, 1·8; 3rd, 6·6; 4th, 3·4; 5th, 5·8; and 6th, ending at the harvest, July 23rd, 4·2.

The control solution (A) yielded plants with good tops and bright, attractive radishes of a light blood-red colour. Nitrogen deficiency (B) resulted in small, undeveloped, but well-proportioned plants, the radishes being about 0·6 cm. in diameter. The cotyledons showed a red outline which was found in further experiments to be characteristic of nitrogen deficiency for this crop, at least for this variety of it; even the central veins were flushed with red. The roots were paler and not so attractive looking as those of the controls. Deficiency of phosphorus (C) resulted in smaller, less-developed plants than the controls, with roots not so uniform in colour. Potash deficiency (D) yielded plants with tops about equal in size to those of the controls, of lighter green colour, but smaller roots of the same attractive colour. Calcium deficiency (E) resulted in plants not quite so large as the controls, with tops slightly lighter green and of a more upright habit of growth, and roots of the same attractive colour. A deficiency of magnesium (F) yielded plants about equivalent in size to the controls but of a much more pronounced upright habit of growth. The tops were a little lighter in colour than those of the controls, but the roots were similarly coloured.

THE DATA OBTAINED FROM THE DIFFERENT TREATMENTS.

Eleven numerical values were obtained for each plant, viz., the fresh weight in grams of the top (cut off at the junction with the root or bulb of the vegetable); of the root (which was arbitrarily taken, as in horticultural practice, to be the edible part of the carrot, onion, or radish, plus associated fibrous roots); of the total plant; the corresponding dry weights; the top/root ratio for dry and fresh weights; and the percentage moisture content of the fresh material of the top, root, and total plant.

The actual data of the experiment are too bulky to be published here, but they are available for examination in the laboratory of this Station. Analyses of variance (3) were worked out for all the eleven values mentioned above. The corresponding summaries of results are set out in Table II together with the standard errors of the treatment means (3). Arithmetical and not weighted means have been used when dealing with ratios and percentages (5).

In the first column, Description of Data, FW and DW denote fresh and dry weights respectively. Opposite each entry in this column there also occurs

TABLE II.

Summaries of Results.

CARROTS.

Description of Data.			Treatment Mean for : A.	B.	C.	D.	E.	F.	Mean of all Results.	S.E.
Tops	FW.	SSS.	7·95	0·264	0·769	8·03	5·48	7·20	4·949	0·5480
			A=D=F>E>B=C.							
Roots	FW.	SSS.	30·56	0·919	4·187	25·62	18·40	23·94	17·27	2·966
			A>E>B=C ; A=D=F ; D=E=F>B=C.							
Total Plants	FW.	SSS.	38·50	1·183	4·956	33·65	23·88	31·14	22·22	3·362
			A>E>B=C ; A=D=F ; D=E=F>B=C.							
Tops	DW.	SSS.	1·173	0·048	0·164	1·211	0·994	1·240	0·805	0·0909
			A=D=E=F>B=C.							
Roots	DW.	SSS.	2·917	0·091	0·417	2·461	1·830	2·351	1·678	0·2814
			A>E>B=C ; A=D=F ; D=E=F>B=C.							
Total Plants	DW.	SSS.	4·090	0·139	0·581	3·672	2·824	3·593	2·483	0·3547
			A>E>B=C ; A=D=F ; D=E=F>B=C.							
Top/Root	FW.	NS.	0·324	0·408	0·208	0·376	0·581	0·406	0·3838	0·0958
Top/Root	DW.	S.	0·483	0·622	0·440	0·585	0·756	0·649	0·5892	0·0735
			A=B=C=D=F ; E>A=C ; B=D=E=F.							
Tops ; % Moisture ..		SSS.	85·34	81·24	77·76	84·83	81·29	82·70	82·20	0·5369
			A=D>B=E=F>C.							
Roots ; % Moisture		NS.	90·34	88·13	89·81	90·41	87·65	89·72	89·34	1·028
Total Plants ; % Moisture		SS.	89·20	86·40	87·86	89·00	86·75	88·02	87·87	0·5745
			A=C=D=F ; A=D>B=E ; B=C=E=F.							

ONIONS.

Description of Data.			Treatment Mean for : A.	B.	C.	D.	E.	F.	Mean of all Results.	S.E.
Tops	FW.	SSS.	27·63	3·56	6·44	10·11	17·70	18·69	14·01	6·047
			A>B=C ; A=D=E=F ; B=C=D=E=F.							
Roots	FW.	SSS.	99·17	13·34	9·48	42·74	55·72	57·07	46·25	7·720
			A>D=E=F>B=C.							
Total Plants	FW.	SSS.	126·8	16·90	15·92	52·85	73·42	75·76	60·26	10·21
			A>D=E=F>B=C.							
Tops	DW.	SSS.	6·030	0·480	0·917	3·480	5·360	4·840	3·516	0·3948
			A>F>D>B=C ; A=E>D ; E=F.							
Roots	DW.	SSS.	20·17	2·820	1·375	7·450	13·35	8·620	8·964	2·142
			A>E>B=C ; A>D=E=F ; B=C=D ; E=F>C.							
Total Plants ..	DW.	SSS.	26·20	3·300	2·292	10·93	18·71	13·46	12·48	2·367
			A>E>D>B=C ; A>F ; E=F>B=C ; D=F.							
Top/Root	FW.	SSS.	0·268	0·261	0·733	0·297	0·363	0·270	0·3636	0·0639
			C>A=B=D=E=F.							
Top/Root	DW.	SSS.	0·414	0·253	0·821	0·705	0·822	0·595	0·6016	0·09279
			A=F ; C=D=E>A=B ; C=D=E=F>B.							
Tops ; % Moisture ..		SSS.	69·99	79·64	79·38	58·50	65·18	60·33	68·84	3·534
			A=B=C>D ; A=E=F ; B=C>D=E=F.							
Roots ; % Moisture		S.	80·47	78·69	85·83	83·67	80·22	84·96	82·30	1·860
			A=C=D=F ; A=B=D=E ; A=D=E=F ; C>B=E ; F>B.							
Total Plants ; % Moisture		SS.	78·67	78·98	85·02	79·11	76·29	81·10	79·86	1·570
			C>A=B=D=E ; A=F ; C=F>E.							

RADISHES.

Description of Data.			Treatment Mean for: A.	B.	C.	D.	E.	F.	Mean of all Results.	S.E.
Tops	FW.	SSS.	2·023	0·231	1·019	2·308	1·718	2·070	1·562	0·0979
			A=D=F>E>C>B.							
Roots	FW.	SSS.	2·459	0·094	0·696	1·218	2·042	2·688	1·533	0·1765
			A=F>C−D>B; A=E; F>E>C=D.							
Total Plants ..	FW.	SSS.	4·481	0·325	1·715	3·526	3·760	4·758	3·094	0·2273
			A=F>D=E>C>B.							
Tops	DW.	SSS.	0·158	0·032	0·093	0·165	0·136	0·154	0·123	0·0077
			A=D=F>C>B; A=E=F>C; D>E.							
Roots	DW.	SSS.	0·139	0·019	0·057	0·082	0·108	0·132	0·0895	0·0079
			A=F>E>D>C>B.							
Total Plants	DW.	SSS.	0·297	0·051	0·150	0·246	0·244	0·286	0·2123	0·0131
			A=F>D−E>C>B.							
Top/Root	FW.	SSS.	0·906	3·159	1·990	2·754	1·070	0·843	1·787	0·2686
			B>C>A=E=F; B=D; C=D>A=E=F.							
Top/Root	DW.	SSS.	1·149	1·705	1·748	2·362	1·423	1·246	1·606	0·1446
			A=E=F; B=C>A=F; D>B=C=E; D>A.							
Tops; % Moisture ..		SSS.	92·23	86·08	90·90	92·90	92·09	92·45	91·11	0·2629
			A=E=F>C>B; A−D=F; D>E>C.							
Roots; % Moisture		SSS.	94·01	73·64	90·06	92·30	94·39	95·00	89·90	1·147
			A=D=E=F>B; A<C; C=D>B; F>C.							
Total Plants; % Moisture		SSS.	93·31	83·06	90·94	92·91	93·38	93·93	91·26	0·3595
			A=D=E=F>C>B.							

one of the descriptions, S, SS, SSS or NS. These indicate that the treatment means concerned were found to be significant by the z test at the 5%, 1% and 0·1% levels, or were not significant, respectively. Treatment means are recorded under the A-F column subheadings. The mean of all the results for a sub-table (which is here also the mean of the treatment means) is placed in the next column, and the standard errors of the treatment means are given in the last one. Where the results for a sub-table are significant, a second line is given which contains a summary of the comparisons of significance of the treatment means; the signs = and >, connecting any two treatments, are to be read as "not significantly different from", and "significantly greater than", respectively.

DISCUSSION OF RESULTS.

The important comparison is that between the data for the plants in each solution and those for the control plants (A), as this gives the effect of the deficiency of each particular element. Less important comparisons which can be made are those between the plants in the solutions generally. For instance, the effect of deficiency of nitrogen on a crop as compared with that of phosphorus.

Carrots.

Deficiencies of nitrogen and phosphorus. As regards both fresh and dry matter, solutions B and C depressed the yields of tops, roots, and total plants, much below those of plants in the control solution (A). Top/root ratios for the dry weights, where the results were significant (S), were uninfluenced (A=B=C). The percentage of moisture in the tops was significantly reduced by the deficiency of each element, but the results for the roots were not significant; the reduction for the total plant was significant for nitrogen, but not for phosphorus.

With *deficiency of potassium,* D=A for the fresh and dry weights of tops, roots, and total plants, demonstrating that little available potassium was necessary for good growth, that the sand and/or the pots were furnishing some of it, or that the sodium present in the sodium phosphate and sodium nitrate used in making up the solutions was replacing it to some extent (2). As with May King lettuces (6), little available potassium seemed to be necessary for good growth with this variety of carrot, and deficiency symptoms seemed to precede diminution in yield (1). The top/root ratio for dry weights, and the moisture content of the various parts were also unaltered. Very similar remarks apply to *deficiency of magnesium* (F).

The diminished amount of calcium (E) caused a significant decrease in the fresh weights of tops, roots, and total plants, and significantly reduced the dry matter of the roots and total plants, but not the dry matter of the tops.

Onions.

Deficiencies of nitrogen (B) and *phosphorus* (C) resulted in greatly diminished yields of the fresh and dry matter of tops, roots, and total plants. The top/root ratios with phosphorus deficiency were significantly increased, top growth being increased relatively to the onion bulb itself. The same ratios were not significantly reduced by deficiency of nitrogen. Nitrogen deficiency caused no change in the moisture content of the tops, roots, and total plants (B=A), but with phosphorus deficiency the moisture in the total plant, though not in its separate parts, was significantly increased.

Deficiency of potassium (D) caused a comparatively large reduction in the fresh tops which, however, was just not significant. The reductions were significant for the roots and total plants (D<A), but even so it will be noted that once again a moderately large plant was obtained with a small amount of available potassium. The percentages of dry matter were all significantly reduced. The top/root ratio for fresh weights was not altered (D=A), but was increased for the dry matter (D>A). The moisture content for the roots and total plants remained unaltered (D=A), but that of the tops was significantly decreased.

With *deficiency of calcium* (E) and of *magnesium* (F) the reductions in the fresh tops were also not significant; but those for the roots and total plants were significant again, as with potassium deficiency. The reduction in dry matter of the tops was significant for magnesium but not for calcium; with roots and total plants, however, the reductions were significant (E=F<A). The top/root ratios for the fresh weights were not significantly influenced by the deficiency of either element; but, though the same result was recorded for the dry matter for magnesium, the ratio for calcium was significantly increased (E>A). The moisture content of the tops, roots, and total plants, was not significantly altered by the deficiency of either element.

Radishes.

Deficiency of nitrogen (B) depressed the yields of fresh and dry matter below those of the control plants (A) very markedly for roots, tops, and total plants. The top/root ratios were both increased, and the moisture content of the tops, roots, and total plants, was significantly lowered in each instance.

Smaller but significant decreases in the fresh and dry weights of the tops, roots, and total plants, resulted from *deficiency of phosphorus* (C). For roots in general, evidently, as opposed to a leaf-crop such as lettuce (5), a great quantity of available phosphate (or alternatively a low N/P ratio) is not necessary. The two top/root ratios were both significantly increased, and the moisture content figures of the tops, roots, and total plants, were significantly lowered.

Results for *deficiency of potassium* (D) emphasized the fact that little of this element is necessary in sand culture work. Thus, the fresh weights of the tops were equivalent to those of the control plants (A), and the yield of roots, though significantly less, was equal to half that of the control. The yields of total plant, although good, were also significantly less. Very similar relations were obtained for the dry matter yields. The two top/root ratios were both significantly increased, but there was no significant influence on the moisture content of the tops, roots, or total plants.

The amounts of available calcium and magnesium needed were evidently small. Thus, with *deficiency of magnesium* (F) the yields of tops, roots, and total plants, both as fresh or dry matter, were not significantly different from those of the control plants (A); the two top/root ratios and the three moisture content figures were also uninfluenced. In fact, the reduction of magnesium to this small quantity was absolutely without any significant effect at all.

With *deficiency of calcium* (E) the fresh weights of the tops and total plants suffered small but just significant reductions, while that for the roots was not statistically altered. The dry matter of the tops was unaltered, but that for the roots and the total plants suffered small, but just significant, reductions. The two top/root ratios and the three moisture content figures were uninfluenced by the deficiency.

ACKNOWLEDGMENT.

The author thanks Mr. T. W. McKean for his great help during the routine work of the experiments.

SUMMARY.

Observations on the behaviour of the root crops, carrot, onion and radish, grown in sand culture, are recorded. Deficiency symptoms are described, and quantitative data as to the yields and ratios of the different parts of the plants are tabulated and statistically examined.

Lack of potassium produced in general a tendency to scorch and wilt of portions of the tops of the plants. Deficiency of nitrogen resulted in onion tops of a very pale green colour, and in a very characteristic outlining in red of the cotyledons of the radish plant. With the solutions used and under the conditions described, the deficiencies of nitrogen and phosphorus resulted in greatly diminished yields. The reductions in yields with the solutions containing small amounts only of the elements potassium, calcium, and magnesium, however, were much smaller.

REFERENCES.

(1) *Eckstein, O., Bruno, A.* and *Turrentine, J. W.* Potash deficiency symptoms. Verlagsgesellschaft für Ackerbau. Berlin, 1937, Plates 36 and 37; p. 5.

(2) *Miller, E. C.* Plant Physiology. McGraw-Hill, 1931, pp. 254; 282-3.

(3) *Wishart, J.* and *Sanders, H. G.* Principles and practice of field experimentation. The Empire Cotton Growing Corporation, 1935, pp. 15 *et seq*.

(4) *Woodman, R. M.* Pure silica sand as a basis for phosphate deficiency tests on lettuce. Sands, Clays & Minerals, 1936, **3**, 22.

(5) ———. Studies in the nutrition of vegetables. Phosphate deficiency and yield tests on sand cultures of May King lettuce. Journ. Agric. Sci., 1939, **29**, 229.

(6) ———. The effects of variation in the supply of potash to lettuces grown under glass. Journ. Pom. & Hort. Sci., 1939, **17**, 167.

(*Received* 9/6/39.)

FIELD SAMPLING FOR THE COMPARISON OF INFESTATIONS OF STRAWBERRY CROPS BY THE APHIS *CAPITOPHORUS FRAGARIAE* THEOB.

By R. M. GREENSLADE and S. C. PEARCE
Horticultural Research Station, East Malling

Introduction.

In ecological studies of insects it is desirable to have a precise method of expressing the degree of abundance of a species in the field, and as it is impossible to count the whole population it is usual to take a standard sample from it. This may be obtained by counting the insects on a given number of leaves or plants, or within a given small area, or by counting the insects obtained in a number of sweeps with a standard net. A series of samples representing with known accuracy the populations from which they are taken will then enable comparison to be made between the density of populations existing under differing ecological conditions. In the present paper an account is given of a search for a method of comparing populations of the Strawberry Aphis, *Capitophorus fragariae* Theob., which, because it transmits virus diseases from plant to plant, is the most serious pest of commercial strawberry fields. In common with most aphides, this species is not always equally prevalent, and the occasional marked lack of infestation is sufficient reason for an ecological study of the species ; but in order to do this a fairly accurate sampling method is a necessity.

Existing Sampling Methods Applied to Strawberry Aphis.

It is an advantage for field sampling methods to be rapid, so that the same observer may be able to sample a number of places within a very short time. This is especially necessary with aphides, which increase so rapidly at certain seasons. For this reason the first method tried for Capitophorus was visual estimation of the population of a number of individual plants chosen at random from the field. To test the accuracy of the method each plant of a block of thirty was examined and placed in one of five categories according to its degree of infestation. Four observers made records of the same plants and repeated the examination four days later. The method was rapid, thirty plants being examined and the figures recorded in fifteen minutes ; but correlation between observers was very low, as was that between the duplicate examinations by the same observer. It was obvious that in spite of having standards agreed on by consultation between the observers, their mental impressions of the categories

differed and were not constant from day to day. An attempt was made to improve the method by examining and estimating separately each quarter of the plant, but this was found to be impracticable. A good sampling method must allow only the least possible personal error, hence the estimation method was rejected.

The next method considered was that used by W. M. Davies in his studies of potato aphides, in which actual counts of the insects were made (3, 4). By that method the potato field was traversed twice, in opposite directions, fifty leaves being picked each time from all parts of the plants. The number of aphides counted on these leaves was called the index figure. It served to compare one field with another and, by further work, to estimate the actual population of the field. This method could not be applied without modification to the Strawberry Aphis since this species has very different habits from those of the potato aphides. The Strawberry Aphis is not evenly distributed over the plant, but lives mainly on the young leaves just coming from the crown of the plant and moves off them as they open, so that a sample of young leaves will best represent the population of these aphides. Capitophorus also differs from the potato aphides in that it is usually less evenly distributed in the field, so that a simple traverse is not sufficient, and sample leaves must be picked at random from the whole field.

Statistical Examination of Data Obtained from Leaf Counts.

A disadvantage of the data obtained by counting the aphides on sample leaves is that differences which are equal in magnitude are not necessarily of equal significance. Thus, the difference between one aphis on a leaf and none at all is more significant than the difference between eleven and ten, which in turn is more significant than the difference between 101 and 100; yet all would have an equal effect on an estimate of infestation by the total population of certain sample leaves. This disadvantage arises because the variation between plants increases with the level of population, thereby diminishing the significance of any given difference. The appropriate procedure is to *transform* the data, that is to use some simple function of them that will have equal variance at all values of its range. For example, Bartlett (1), working with the numbers of cockchafer larvae occurring in plots of standard size, measured his infestation not by the population, n, but by either $\sqrt{n}$ or $\sqrt{n+\frac{1}{2}}$. Cochran (2), who has given a general discussion of the properties of transformations, found another use for $\sqrt{n+\frac{1}{2}}$, when dealing with counts of wireworms, while Williams (5) made use of $\log(n+1)$ with the number of moths caught in a light trap.

In order to investigate the most suitable method for use with the number of strawberry aphides on sample leaves, three uniformity trials were planned.

All were concerned with a plot of Royal Sovereign strawberries consisting of five rows of 100 plants each, running from north to south, planted two years previously. At three seasons of the year (in October, April and June) one young leaf was chosen at random on each plant, and the aphides upon it were counted without picking it. From the figures obtained a calculation was made of the error with which one of the leaves would have provided an estimate of the mean infestation of the whole plot on each of the three occasions, in order to determine whether this error was more constant with actual counts or with transformed data. Two transformations were tested (i) $\sqrt{n+\frac{1}{2}}$, because Bartlett (1) had shown its value in dealing with a Poisson distribution, which the aphis counts were expected to follow, and (ii) *log* $(n+1\frac{1}{2})$, because for large values it approximates to *log* n, which is a standard transformation, and for small values is equivalent to $\sqrt{n+\frac{1}{2}}$. The results of these uniformity trials are set out in Table I, which shows the estimated standard deviations of an individual observation, as well as the means of the observations.

TABLE I.

Mean and standard deviation of leaf counts, using actual counts and two transformations.

Data.	n		$\sqrt{n+\frac{1}{2}}$		*log* $(n+1\frac{1}{2})$	
	Mean per leaf.	S.D.	Mean per leaf.	S.D.	Mean per leaf.	S.D.
October	6·78	7·62	2·39	1·25	·77	·36
April	7·77	8·86	2·53	1·37	·81	·39
June	14·57	10·61	3·66	1·30	1·33	·29

It will be seen that using actual counts the expected has occurred, the standard deviation being greater when the level of population is high, while the transformation *log* $(n+1\frac{1}{2})$, on the other hand, has been too drastic and has unduly depressed the June variation. The intermediate, $\sqrt{n+\frac{1}{2}}$, has proved the most satisfactory* and will be used throughout the present paper. The number of aphides, n, upon a leaf will be termed the "population count", and the quantity $\sqrt{n+\frac{1}{2}}$, the "population index". Attention will be directed to a method of obtaining a sample of leaves such that the mean index of the sample shall provide an estimate of the mean index of all the leaves of the field.

* For the purposes of the present paper the form of distribution of the transformed variate is irrelevant, for it is proposed to deal only with means of large samples, and these will be approximately normal variates whatever the distribution of their components may be. Actually the closest approach to normality was given by *log* $(n+1\frac{1}{2})$.

DESCRIPTION OF THE SUGGESTED METHOD OF SAMPLING.

The size of sample that can be used is, in practice, always limited by the time at the observer's disposal, and the best procedure therefore is to approach a field with the intention of examining only a certain number of leaves from it ; otherwise the observer will begin at one end, find that he is spending too much or too little time there and then alter the distance between his leaves, thereby taking an unevenly distributed sample. Suppose that there are about 20,000 plants and that time allows only about 50 leaves to be examined ; then, not more than one leaf can be chosen from every 400 plants. Obviously it would be very laborious to divide the field into blocks of this size and to choose one leaf purely at random from each, hence it is suggested that sampling should proceed as follows: Take 400 plants (say, 20 by 20) in one corner of the field, and select one plant at random in it, and from that plant take one young leaf, also at random. Then proceed up the row from this plant, taking leaves from the 20th, 40th, 60th plant, and so on, until the end of the row is reached at, say, the 12th plant beyond the last one sampled. Move across 20 rows and begin to work back, still taking leaves from every 20th plant, beginning in this example at the 8th plant. Gaps should be included in the counting, in order to ensure having blocks of equal area. In this way the recorder will traverse a zig-zag course across the field taking leaves at regular intervals ; and though he will not obtain a truly random sample, the variation in aphis populations can be shown to be of so local a character that no serious error should arise. This procedure has the effect of dividing the field into a number of imaginary blocks each of which is represented by one leaf.

When this method was actually tried, the leaves were at first picked, the aphides counted and the numbers of them recorded in the field. But many more samples can be taken if it is not necessary to count in the field. Later, therefore, the leaves were placed in numbered glass tubes, and the counting was done in the laboratory. Furthermore, this enabled a binocular microscope to be used, which is an advantage where other species of aphides are mixed with Capitophorus. The leaves can be kept for three or four days if necessary, as it is quite possible to count dead aphides ; but they must not be allowed to become mouldy. A further modification of the method was found possible which allowed samples of leaves to be kept longer than a few days before counting. The leaves were picked and placed in small numbered envelopes, of the type generally known as wages packets, sealed and allowed to dry. Mould is thus avoided and the dry leaf in its envelope can be stored for any reasonable length of time. When it is necessary to count the aphides, the sealed envelopes are placed a few at a time under an inverted beaker over a water bath. The steam softens the envelope and leaf, the envelope is opened out flat and the aphides counted under the binocular microscope. Care should be taken not to " cook "

the leaf, since if it becomes wet, it is difficult to see the aphides. This method is of course much slower than dealing with fresh leaves, but it enables the recorder to take a large number of samples without returning to the laboratory at a busy season when time for counting cannot always be found. It would also allow of samples being sent by post, if desired, as the leaf can be pressed flat and one hundred leaves in envelopes occupy less space than twenty 3 in. × 1 in. tubes.

Estimation of Error of the Method.

In order to determine the accuracy of this method it is necessary to know how well the population index of one leaf estimates conditions over the whole of the block from which it was taken. The population indices obtained from the 500 plants were examined in order to determine the standard deviations within blocks of various sizes running across the original block. The results are set out in Table II.

Table II.

Estimates of standard deviations of population indices within blocks across the original block.

Size of Block	5	10	25	50	100	250	500 plants.
October ..	1·15	1·16	1·17	1·17	1·18	1·23	1·25
April	1·30	1·28	1·30	1·30	1·31	1·37	1·37
June	1·28	1·25	1·24	1·24	1·24	1·25	1·30

It will be seen that the variation is extremely local, the largest blocks being scarcely more variable than the smallest. It will be noticed, too, that the smallest blocks are not always the most uniform ; this can be explained by a headland effect, the outside plants being rather less infested in April, and much less infested in June than the inside ones. Since 40% of the plants were in the headlands, this effect was of some importance. Table II was therefore recalculated using blocks taken along the rows and containing wholly outside or wholly inside plants. Although this division gave very long, narrow blocks, they were mostly more uniform than the more compact ones used for Table II. As Table IIa shows, these recalculated variations are greater in the larger blocks, with one exception in October.

From Tables II and IIa it appears that the standard deviation within blocks of any size up to 500 plants usually does not exceed 1·30. Assuming this to be the usual extent of variation, it follows that if n_1 leaves are taken from a field in the manner described (there being at least one leaf from every 500 plants)

TABLE IIA.

Estimates of standard deviations of population indices within blocks along the original block.

Size of Block	5	10	25	50	100 plants.
October	1·17	1·15	1·17	1·22	1·24
April	1·24	1·28	1·30	1·34	1·36
June	1·04	1·08	1·10	1·11	1·17

and these leaves have a mean population index of i_1, and if n_2 leaves from another field have a mean index of i_2, then the difference between i_1 and i_2 will exceed $2{\cdot}6\sqrt{\frac{1}{n_1}+\frac{1}{n_2}}$ only once in twenty times if the fields are equally infested.*

To take a numerical example: Suppose that the sampling of 20,000 plants as described above had given a sample of 50 leaves with a mean population index of 2·50, and on repetition one of 2·75, would this be evidence of a change in population between the two samplings? The answer is "No", because the limits of chance variation between two samples of 50 is $2{\cdot}6\sqrt{\frac{1}{50}+\frac{1}{50}}$, or ·52, and the actual difference was only ·25. Since a difference of ·52 can be exceeded by chance on 5 occasions out of 100, even an actual difference of that magnitude would not have been conclusive, but it would have been strong evidence.

The question does, however, arise whether the standard deviation of 1·30 derived from Tables II and IIA is of general application. Probably it is an over-estimate, because the 500 plants used for the uniformity trials had been "gapped up" in the previous year with plants taken from an extension of the same field, and consequently having infestations different from those which would ordinarily be expected from their final positions. The large proportion of the field in the headlands has already been referred to, and this undoubtedly increased the variability. The accuracy of the method has therefore probably been underestimated.

* If the standard deviation of an individual is 1·3, the standard error of the difference between two means is $1{\cdot}3\sqrt{\frac{1}{n_1}+\frac{1}{n_2}}$; but purely by chance the means of two samples taken from the same or similar populations differ by more than twice the standard error of their difference only once in twenty times, provided that enough data have been used in the calculation. If, then, the difference between i_1 and i_2 is found to exceed $2{\cdot}6\sqrt{\frac{1}{n_1}+\frac{1}{n_2}}$ either the twentieth chance has happened, or there is in fact a real difference.

SIZE OF SAMPLE IN PRACTICE.

In deciding on the size of the sample there are two things to be noted: (i) that no information has been obtained about the variation within blocks of more than 500 plants, therefore at least one leaf must be taken from each block of that size ; (ii) that the transformed variate is not normally distributed, and that it is therefore desirable to have at least twenty-five leaves in the sample to overcome the asymmetry of the variate. So small a sample, however, would show only differences that a competent recorder could detect by observation, and an arbitrary sample of seventy was adopted which proved satisfactory. It shows smaller differences without being unduly laborious. By taking a sample large enough it is possible to prove any real difference, though the extra accuracy obtained by taking samples of more than 100 hardly compensates for the labour involved. This is a matter that every experimenter must decide for himself, but in general it is recommended that such large samples should be used only when the size of the field demands it, i.e. when there are more than 50,000 plants. It is also desirable to use blocks as compact as possible.

TRIAL OF THE METHOD IN THE FIELD.

In order to test the method in practice three trials were carried out. The first was at East Malling in January, and consisted of six comparable samplings

TABLE III.

Population counts and indices obtained from six comparable samples from the same field.

No. of Sample.	Size of Sample.	Mean Population Count.	Mean Population Index.
I.	31	·74	1·01
V.	30	·73	·95
IV.	27	·67	·95
II.	31	·48	·93
III.	34	·35	·86
VI.	29	·14	·78

from a 4 acre runner bed. The field was long and irregular, and the rows were taken along it. This was unfortunate because it resulted in samples of varying sizes depending on the starting point. For each sampling, one leaf was taken from each block of 484 plants (22×22). The results are set out in Table III, the samples being arranged in order of the mean indices they gave.

Since in six samples there are fifteen pairs, and in none of them does the difference found even approach significance, this trial suggests that the method is more accurate than the calculation from the uniformity trials has suggested. This is not to be explained by the use of a runner bed, for the wider spacing

in such a field would be likely to increase the variation within a block occupied by a given number of plants. This trial also indicates that variability is no greater at very low infestations such as this one.

The second trial consisted of duplicate samples taken at the end of June and the beginning of July from three fields in different parts of Kent, at Wateringbury, Westerham and East Farleigh. The block size was 20×10 at Westerham where about $1\frac{1}{4}$ acres had to be surveyed, and 20×20 at the other two places, where the area was about twice as large. The results are given in Table IV.

TABLE IV.

Duplicate samples from commercial plantations in Kent.

Sample.	Size of Sample.	Mean Population Count.	Mean Population Index.
Wateringbury I. ..	70	12·66	3·28
II. ..	70	14·80	3·52
Westerham I. ..	70	5·73	2·25
II. ..	70	6·51	2·42
E. Farleigh I. ..	70	4·46	1·67
II. ..	70	2·04	1·30

The significant difference for two samples of seventy is ·44, and it appears that no pair of duplicate samples failed to agree, while all three fields differed significantly, irrespective of the sample by which they were represented.

At the end of July and the beginning of August duplicate samples were taken from fields at Drumorgan and Druminnis in Northern Ireland. The practice in that district is to grow strawberries in a matted row ; it was therefore impossible to count plants in order to space the sample, and a standard distance was used instead. Leaves were taken every four yards from every third row, the blocks being therefore of a size that would, under Kentish conditions, contain about thirty plants. Both fields were of about $\frac{1}{4}$ acre. The results are shown in Table V.

TABLE V.

Duplicate samples from commercial plantations in Northern Ireland.

Sample.	Size of Sample.	Mean Population Count.	Mean Population Index.
Druminnis I. ..	70	1·03	1·13
II. ..	70	1·33	1·22
Drumorgan I. ..	70	·70	·98
II. ..	70	·97	1·08

No significant difference was found between members of either pair, or indeed between any of the four samples.

The cumulative evidence of these three trials is that the population index is a more stable estimate of infestation than the population count, and that the difference between like samples does in fact only rarely exceed $2{\cdot}6\sqrt{\frac{1}{n_1}+\frac{1}{n_2}}$. Both of these results were foretold by the uniformity trials.

Limitations and Potentialities of the Method.

The method described here does not at present allow comparison to be made between different varieties of strawberries. The distribution of the aphis population between young and old leaves is not the same with all varieties, so that the complete population of a number of plants must be examined and the relation between the population of the sample leaf and that of the whole plant must be determined. It should then be possible to sample all varieties and compare their aphis populations. That is to say, the effect of variety may be eliminated. The same method should allow comparison to be made between plants of different ages, though it is not anticipated that there would be much difference due to this factor except between one and two year old plants. In order to observe the seasonal change of population the same method would probably be necessary. The method does, however, allow comparison to be made between plants of the same age and variety. Although very small differences cannot be detected with a sample of reasonable size, yet it was possible by the field samples of seventy leaves to show differences which were not apparent to the eye. The ability to do this is especially useful where several hours or even a day or two elapse between visiting two fields, and when the mental impressions of the degree of infestation cannot be retained with certainty. The relative degree of aphis infestation in different districts could be determined by taking samples from several fields in each district at approximately the same time. A series of samples taken at intervals would probably show whether any real difference existed between the quantities of aphides in the different areas. The error of sampling being stabilized, there is no reason why further work should not increase the sensitivity of the method and enable much smaller differences to be detected. This would make it possible to observe the effect on aphis population in the field of many ecological conditions and so to increase knowledge of the biology of the strawberry aphis. Even if this pest can be completely eliminated from new plantations, in the crowded conditions existing at present in strawberry growing areas there is always the chance of its re-introduction ; hence it would be wise, if possible, to avoid growing strawberries under conditions conducive to the rapid spread of this disease-carrying aphis.

The writers are indebted to Mr. T. N. Hoblyn for his advice on many aspects of the work presented in this paper.

SUMMARY.

An account is given of a search for a method of sampling the population of *Capitophorus fragariae* Theob. in strawberry fields.

The method devised consists of counting the aphides on a number of sample leaves, one leaf being taken from each of a number of equal sized blocks into which the field is divided.

It is shown that the quantity $\sqrt{n+\frac{1}{2}}$, in place of the actual number of aphides on a leaf, n, enables considerably better comparison to be made between different samples.

Evidence is advanced to show that the standard deviation of $\sqrt{n+\frac{1}{2}}$ within a block of less than 500 plants rarely exceeds 1·3.

REFERENCES.

(1) *Bartlett, M. S.* The square root transformation in analysis of variance. Journ. Roy. Stat. Soc. Suppl., 1936, **3**, 68-78.

(2) *Cochran, W. G.* Some difficulties in the statistical analysis of replicated experiments. Empire Journ. Exp. Agric., 1938, **6**, 157-75.

(3) *Davies, W. M.* Ecological studies on aphides infesting the potato crop. Bull. Ent. Res., 1932, **23**, 535-48.

(4) ———. Studies on aphides infesting the potato crop. Ann. Appl. Biol., 1934, **21**, 283-99.

(5) *Williams, C. B.* The use of logarithms in the interpretation of certain entomological problems. Ann. Appl. Biol., 1937, **24**, 404-14.

(*Received* 12/9/39.)

MOSAIC DISEASE OF THE RASPBERRY IN GREAT BRITAIN

II. EXPERIMENTS IN TRANSMISSION AND SYMPTOM ANALYSIS

By R. V. HARRIS
East Malling Research Station

INTRODUCTION.

THE first paper in this series (11) was a summary of field observations made from 1921 to 1932 on symptoms and on apparent relative varietal susceptibility. A range of Mosaic leaf symptoms was distinguished, varying from a faint and evenly distributed mottle to a sharply defined chlorotic speckle with pronounced laminal distortion, and, for convenience of description, these were referred to three symptom types, *a, b* and *c*.

In 1925 a successful attempt was made to graft raspberry canes, and in the following year Mosaic symptoms were transmitted to normal plants by this means. This result was confirmed by a further experiment in 1927. Numerous attempts from then onwards to transmit by other and mechanical methods and to discover alternative and differential hosts have so far been without success, and parallel investigations by the Station Entomologists on possible insect vectors have also yielded inconclusive results. Transmission by grafting has therefore been the only method employed for the analysis of the observed range of field symptoms on an extensive collection of commercial varieties. Such an experimental analysis has been in progress from 1928 onwards, and the experiments, together with the initial transmissions in 1926-27, form the main subject of the present communication.

From 1933 to 1934 the writer was in temporary residence in Eastern Canada at the Dominion Laboratory of Plant Pathology, St. Catharines, Ontario.* Here, preliminary experiments were made in the direct comparison of the virus diseases of the raspberry in Great Britain and in North America by the transmission of the latter to healthy plants of two English indicator varieties, using the grafting method adopted at East Malling.

The results, although suggestive, were inconclusive, and further experiments in confirmation and extension were made at St. Catharines and East Malling

* Under an Exchange of Workers arrangement with Dr. G. H. Berkeley of that Laboratory.

from 1934 onwards. The data from these experiments are still incomplete, and the detailed description of this part of the investigation will therefore be deferred for a future communication.

REVIEW OF PREVIOUS LITERATURE.

The following summary is supplementary to that in the preceding paper of the present series (11). Artificial transmission by insect vectors will be discussed solely in its bearing on the etiology of the diseases concerned.

I. North America.

In 1922 Dickson (8) claimed to have transmitted a Mosaic disease to normal red raspberry plants by an aphis thought to be *Aphis rubiphila* Patch. In the same year Rankin and Hockey (15, 16) recorded the transmission of raspberry Leaf-curl by the same aphis. The spread of Mosaic in the field was also correlated by these authors with aphis infestation, but attempts to transmit it by aphides failed. Unsuccessful attempts were also made to transmit Leaf-curl and Mosaic by leaf-rubbing and injection methods.

In 1924 Wilcox and Floyd Smith (21) described the transmission of Mosaic from the red to the black raspberry by the aphis *Amphorophora rubi* Kalt, and Cooley (7) comments, "For several years this reaction of black raspberries was adopted by investigators as the type of what came to be called 'red raspberry mosaic.'"

In 1927 Bennett (2) described successful transmissions of four of his five symptom-types of raspberry virus disease by various species of aphides, the exception being Streak (Eastern Blue-stem). He concluded that Curl and Mosaic diseases are carried principally by different species of aphides (*Aphis rubiphila* and *Amphorophora rubi* respectively), thus providing additional evidence for the etiological distinction of these diseases. Bennett also recorded unsuccessful attempts to transmit Mosaic and Leaf-curl by the direct inoculation of some 300 plants with juice extracted from various parts of diseased plants, by needle puncture, hypodermic needle injections and injections under pressure. Budding experiments and bark-grafts were also tried, but he states, "It has been extremely difficult to obtain union with any transplanted parts and in no case has disease been transmitted by these methods."

In 1932 the same author (4) published an account of an experimental analysis of the complete range of symptoms of Mosaic disease on varieties of red, purple (hybrid) and black raspberries by an extensive series of controlled aphis transmissions to selected indicator-varieties under carefully standardized conditions. On the data obtained, Bennett assigned all the forms of Mosaic disease in Michigan to two main virus groups, *Yellow Mosaic* and *Red Raspberry Mosaic*. The former had the well-defined features of a single-virus disease,

the symptom intensity being constant for each variety. The Red Raspberry Mosaic group, however, comprised all the former Red Raspberry Mosaic and Mild Mosaic symptom-categories of previous workers, and thus represented a wide range of symptom-intensity within single varieties. Bennett concluded that this range of symptoms was probably produced by strains of one virus " in different stages of virulence ".

In 1935, Harris (12), in a brief summary of observations and experiments made at St. Catharines, Ontario, in 1933-34, recorded positive transmissions of the Curl and Mosaic diseases from local varieties of red raspberry to healthy indicator plants of selected North American and English varieties. The transmissions were effected by patch-grafting as used in the experiments at East Malling.

In 1936 Cooley (7), following up the observational symptom-analysis of Rankin (17, 18, 19), described aphis transmissions from plants of the purple (hybrid) variety Columbia showing the so-called Mild Mosaic symptoms, to normal indicator plants of black raspberry varieties. Symptoms characteristic of Red Raspberry Mosaic developed invariably on the latter, thus confirming the tentative conclusion of Rankin and (later) of Bennett that the mild symptom group must be identified etiologically with that of Red Raspberry Mosaic. In these experiments the inoculations from uniformly affected Columbian plants induced a wide range of symptom-severity, both inter-varietal and within single varieties. Cooley concludes that in view of the apparently uniform source of infection " it would seem improbable that more than one virus was concerned or that there could have been present several strains of one virus varying in virulence ". He attributes the observed variations of reaction of the indicator plants mainly to individual differences in environmental climatic and cultural conditions. From the results of his own observations and experiments it is concluded that this entire range of symptoms can be assigned to a single virus. In this he agrees with Bennett (4), who, however, postulates a single virus with multiple strains ; but Cooley maintains that " one strain of this one virus may produce the entire range of other-than-Yellow mosaic symptoms that have been observed on black raspberries in eastern North America ". In conclusion, he recommends the following revised nomenclature for the raspberry Mosaic diseases :—

Raspberry Mosaics (Eastern North America).

Green Mottle Mosaic (or Green Mosaic). Virus 1. A descriptive substitute for the misleading Red Raspberry Mosaic or Red Mosaic, and including the entire range of symptoms other than those due to Virus 2.

Yellow Mosaic. Virus 2. " All investigators are agreed upon the usage of this name. No change is needed or advised."

In 1938, Chamberlain (6) described a further virus disease of the red raspberry, first observed in 1935 on the Cuthbert variety in Ontario, for which he proposed the name Yellow-blotch Curl. The virus nature of the disease and its distinction from the Mosaic and Curl of raspberries was confirmed by patch-grafting transmissions to healthy plants of Cuthbert, to four other local varieties of red raspberry and to the English variety Lloyd George. These varieties showed a wide range of susceptibility, and the effect of inoculations on the most highly susceptible was extremely rapid and severe, the stools frequently dying during the season of inoculation. Attempts to transmit the disease to black raspberries have so far failed.

II. EUROPE.

In 1927 Blattný (5), in Czechoslovakia, mentioned two species of aphides as natural vectors of Leaf-curl and Mosaic respectively, but described no experiments in confirmation.

In 1931 Grainger and Angood (9), working at Leeds, England, claimed to have transmitted Mosaic disease to two wild raspberry plants collected in Scotland for their freedom from leaf mottling. The agents of transmission were aphides (identified by the authors as *Aphis rubiphila*) collected from Mosaic-diseased canes in a local garden and transferred directly to the apparently healthy wild plants. Control plants are stated to have remained healthy. Bennett (4) comments, "This needs confirmation since only two plants were inoculated and only twenty aphides used."

MECHANICAL INOCULATIONS.

Various attempts at transmission by mechanical means have been made by the present author, but with completely negative or inconclusive results. These include the following experiments:—

(1) The injection of fruiting canes and young canes with a water-diluted extract from macerated Mosaic-affected canes.
(2) The continued adpression, by means of glass caps, of macerated tissues of Mosaic-affected canes to the freshly cut surfaces of healthy canes.
(3) The pruning of stools with knives dipped in extract from Mosaic-affected canes.

The method of leaf-abrasion was first tried in 1928 in collaboration with W. Steer. Leaves of healthy raspberry plants were scratched with needles and were then treated with water-diluted extracts of macerated Mosaic-affected canes and with the body juices of various insects (suspected vectors) previously fed on Mosaic-affected stools.

In 1934, at the Dominion Laboratory of Plant Pathology, St. Catharines, attempts were made to transmit the local Mosaics of red raspberry to dwarf

French bean, broad bean, tobacco, tomato, garden pea, sweet pea, red clover and sweet clover, by four methods of leaf abrasion. These experiments were continued at East Malling in 1937 when attempts were made to transmit the English Mosaic diseases to healthy raspberry plants, tobacco (*Nicotiana tabacum*), *N. glutinosa*, *Solanum nodiflorum*, Datura and dwarf French bean by leaf abrasion with finely divided carborundum powder.

INITIAL TRANSMISSIONS BY GRAFTING.

Plant Material and Controls.

The variety Baumforth's Seedling B was selected because leaf symptoms were distinct and an adequate proportion of stools of it in the Research Station collection were apparently healthy.

Throughout 1924, stools with leaf symptoms and stools free from symptoms were marked and kept under observation. The canes produced from the division of the final selection of these stools were planted on experimental plots. Plot 1 comprised alternate plantings of five Mosaic-affected and five healthy stools. Plot 2 was planted with healthy canes only, and was thereafter periodically inspected and rogued for symptoms of Mosaic. The Mosaic-affected plants for the experiments now to be described were dug in the early winter from Plot 1 and the healthy ones from Plot 2.

All these canes were planted singly in pots in a standard greenhouse compost, after which they were cut down so as to leave stubs about 6 in. long, and the pots were plunged in the open for the rest of the winter. In early March they were removed to an unheated greenhouse where they remained until ready for grafting. In the greenhouse the plants were sprayed with nicotine to minimize infestation by insects, red-spider, etc., but no attempt was made to grow them under insect-proof conditions. This was partly owing to lack of adequate greenhouse or cage equipment, but mainly to the great practical difficulty of raising plants sufficiently vigorous for grafting (by the methods then available) under such conditions. Previous experience had shown that raspberries, and in particular Mosaic-affected raspberries, do not grow readily in pots, and to obtain reasonably vigorous growth ample ventilation and lighting are essential. Excessively high summer temperature must also be avoided.

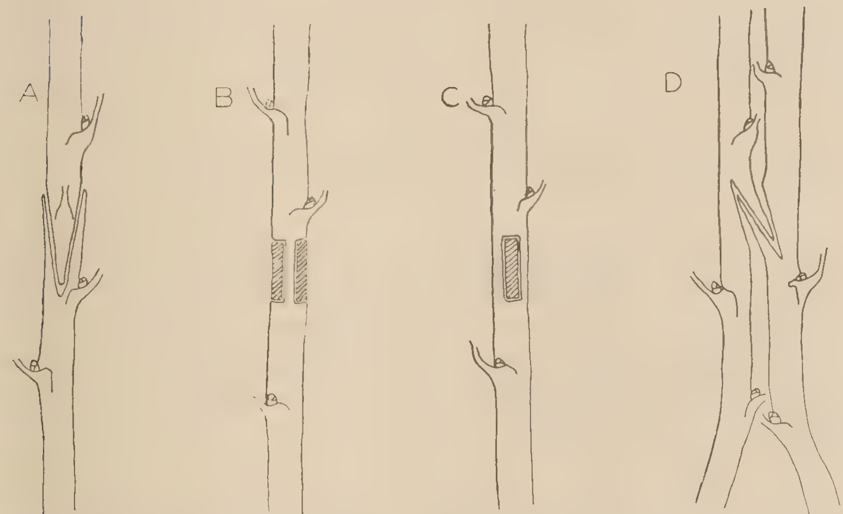
As Mosaic-affected and healthy canes were thus to be grown in close proximity without absolute exclusion of insects, and as the healthy canes were derived from very early selections, the following special precaution was taken to provide adequate control for the experiment. On harvesting the canes from the plots, instead of dividing the plants indiscriminately they were dug and separated in clonal groups, each consisting of three canes root-attached to one another. Each member of a group was labelled distinctively and then potted

singly. The experiments were thus carried out on a number of units of two or three plants comprising one plant available for inoculation and one or two control plants. The appearance of symptoms on any of these controls was countered by the elimination of the appropriate unit from the experiment.

Method of Transmission—Cleft Grafting.

By this method (Text Fig. A and Plate I, Fig. 1) as first attempted, the leafy apical portion of an actively growing first-year (new) cane of the scion-plant was substituted for the corresponding portion of a comparable cane on

TEXT FIGURE.



A—Cleft grafting. B—Patch grafting with ring. C—Patch grafting with panel. D—Cane inarching.

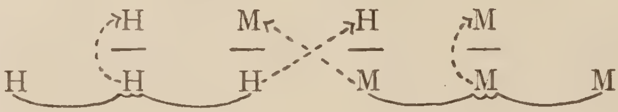
the grafted or stock-plant. An important factor of success was accurate fitting of the scion to the stock, and to achieve this it was advisable to make the cuts in the region where the pith was not yet fully differentiated. The cuts were also made so as to leave a leaf with its axillary bud both on the wedge portion of the scion and on the slotted portion of the stock cane.

The union was bound with Raphia strip and coated with paraffin wax, and the grafted plants were then placed on a bed of moist coconut fibre in a closed greenhouse propagating frame with bottom heat, where they were frequently sprayed with water to prevent flagging. When the axillary scion buds began to expand, approximately one month after grafting, the plants were transferred to closed cold frames for hardening, thence to the bench of a cool greenhouse, then to an outdoor frame and finally to the open ground. The necessarily long

exposure of the plants in hot frames resulted in severe mortality of the grafted canes from Botrytis soft-rot, and the low proportion of successful grafts (a maximum of 45% in 1926) was largely due to this cause. In 1927, successful unions were obtained by simple bell-jar protection of the grafted plants on a cool greenhouse bench, the transpiration of the scion being reduced by cutting off its top, leaving only two leaves on it, and coating its stem with paraffin wax. By this procedure, however, union was considerably delayed and the proportion of successes was lower than in the hot frames.

Experiment 1 (1926).

Each graft unit in this experiment consisted of a clonal group of 3 healthy plants and one of 3 Mosaic-affected plants grafted as shown in the following diagram.*



H clone. M clone.

The inclusion of the ungrafted controls and the $\frac{H}{H}$ and $\frac{M}{M}$ combinations was to determine possible effects due to graft alone. Thirteen graft-units were set up. Owing to shortage of plants the last four units were reduced by omitting the H, $\frac{H}{M}$ and M plants. After grafting and the necessary hardening-off, each unit was plunged in the open ground.

Results. The results are given in Table I and illustrated in Plate II.

The high proportion of plants dying shortly after grafting was due to Botrytis soft-rot set up under the hot closed frame conditions. Union occurred in 24 of the total 48 grafts. The successes were about equally divided between the $\frac{M}{H}$, $\frac{H}{H}$ and $\frac{H}{M}$ combinations. All the control plants persisted free from symptoms with the exception of those of units 4, 5 and 12. In the remainder an apparent transmission of Mosaic symptoms was shown by 7 of the $\frac{M}{H}$ and 5 of the $\frac{H}{M}$ combinations. No transmissions occurred where union failed.

* Graft combinations are conveniently designated as fractions, and the source of the scions by broken lines. Thus $\frac{H}{H}$ indicates a healthy stock-plant upon which is grafted a portion of a cane derived from the same plant. M indicates a plant or scion-cane showing Mosaic symptoms.

TABLE I.

Transmission Experiment 1926.

Graft unit No.	Date of Grafting.	Graft unions.				Symptoms on Controls.		Symptoms transmitted.	
		$\frac{M}{H}$	$\frac{H}{H}$	$\frac{H}{M}$	$\frac{M}{M}$	$\frac{H}{H}$	H	$\frac{M}{H}$	$\frac{H}{M}$
1	27·4	—	—	—	—	D	—	—	+
2	,,	—	+	—	—	—	—	—	—
3	,,	+	—	+	—	D	—	+	+
4	,,	+	—	—	—	+	—	+	D
5	,,	—	—	+	—	+	—	+	+
6	12·5	—	—	—	—	D	—	D	D
7	,,	+	+	—	—	—	—	+	D
8	,,	+	+	+	—	—	—	+	+
9	,,	+	+	—	—	—	—	+	—
10	20·5	+	+	+		—		+	+
11	,,	+	+	—		—		+	D
12	,,	+	+	+		+		+	+
13	,,	+	+	+		—		+	+

+ and — indicate successful and unsuccessful unions or transmissions respectively.
D = Plant died shortly after grafting.

The transmitted symptoms appeared on the leaves of the stock or scion canes within two months after grafting and were generally first detected when the axillary buds of the scion were starting to grow out.

Assuming the transmission of a virus disease through the graft union in the above twelve instances, the absence of symptoms on the ungrafted H plants of the discounted units 4 and 5, and the apparent failure to unite of the infected $\frac{H}{H}$ combination (and on the $\frac{M}{H}$ combination of unit 5) indicate that the grafted H members of each of these units, and probably of unit 12 (not provided with an ungrafted H plant), were already naturally affected at the time of grafting.

EXPERIMENTS 2 AND 3 (1927).

Two experiments were made in 1927 to check the results of the 1926 experiment with special reference to the anomalous $\frac{H}{H}$ grafts, and also to test modifications of grafting method 1 with the object of eliminating the hot frame treatment. Clonal pairs of H plants were used and three types of graft unit set up as follows:—

$$(1)\ \frac{M}{H}, \frac{H}{H}. \qquad (2)\ \frac{H}{H}, H. \qquad (3)\ \frac{M}{H}, H.$$

EXPERIMENT 2.

The grafting procedure of 1926 was closely followed. Of the 17 units set up, however, 16 failed owing to the plants in the hot frames having been

sprayed with an overdose of formaldehyde in an attempt to prevent soft-rot of the scions. In the one successful unit (type 1) the $\frac{H}{H}$ grafted plant remained healthy and the $\frac{M}{H}$ plant developed Mosaic symptoms.

EXPERIMENT 3.

Three modifications of the original grafting method were tried in an attempt to substitute bell-jar protection for the hot frame. One of these was successful and has been described above (page 324). Fifteen units comprising the three types mentioned above were set up, twenty-one plants in all being grafted. Of these, 8 $\frac{H}{H}$ and 6 $\frac{M}{H}$ combinations failed to make union. All the stock-plants of these grafts remained healthy. In the remaining seven, 4 $\frac{M}{H}$ and 3 $\frac{H}{H}$ combinations, union occurred. Mosaic symptoms subsequently appeared on all the stock-plants of the former combinations and those of the latter remained healthy throughout.

GENERAL OBSERVATIONS AND CONCLUSIONS.

(i) THE TYPE OF LEAF SYMPTOMS TRANSMITTED.

Mosaic-affected plants for the above experiments were selected as representative of the type of leaf symptoms then prevalent on the variety Baumforth's B, namely type *b* (11). In nine of the fourteen transmissions type *b* symptoms alone subsequently appeared on the healthy stock-plants and scion-canes. In the remaining five the transmitted symptoms resembled a combination of types *b* and *c*.

(ii) PLANT DETERIORATION.

The appearance of Mosaic symptoms on the stock-plants was invariably associated with a deterioration in their vigour as compared with that of their control plants. Such deterioration was uniformly slow where type *b* symptoms alone were transmitted, but was irregularly rapid where a combination of both symptom types developed. (See Table II and Plate II.)

(iii) GENERAL CONCLUSION.

The above results indicate that Mosaic symptoms on the variety Baumforth's Seedling B are transmissible to healthy plants of the same variety by grafting, and in the absence of any visible pathogen it is concluded that these symptoms are of virus origin.

ANALYSIS OF SYMPTOMS BY GRAFTING.

(Experiments of 1928-1937.)

Having determined the transmissibility of one type of Mosaic symptom on the variety Baumforth's Seedling B by grafting, an analysis of the observed range of symptoms on this and other varieties was undertaken. In view of the negative results of all attempts to transmit by mechanical methods or by insects, grafting was adopted for such an analysis.

The method of cleft grafting used in the first transmissions was inadequate to deal with the enlarged scope of the experiments and a considerable number of experiments were therefore made to find a more suitable one

In the descriptions which follow, certain conventions are adopted. Of the two (or more) members of a graft combination (or unit) the plant to be infected is termed the *indicator* and the diseased plant providing the source of the infection is termed the *infector*. Where cleft grafting or patch grafting were used the indicator was invariably the stock-plant, the scion being derived from the infector.

Plant Material.

Indicator plants and Controls.

For the first experiment in this series (1928) healthy indicator plants (Baumforth's B) were obtained from the plot supplying material for the previous experiments. In addition, the variety Lloyd George was used for the first time, and healthy plants were selected from a recent planting (1926-27) of one of the best commercial strains then available. All detectable Mosaic-affected plants were rogued from a section of this plot in the autumn of 1927, and stools situated at the greatest distance from rogued stools were selected. As in the previous experiments with Baumforth's B, the canes were raised in clonal sets of two, one being used for infection purposes and the other left as an ungrafted control or grafted with a healthy scion.

In the winter of 1927-28 additional plots of Baumforth's Seedling B and Lloyd George were established with apparently healthy canes selected from the above sources and were kept solely for the propagation of disease-free canes for experimental and planting purposes. All first-year canes were inspected and any apparent Mosaic-affected plants rogued and flowering cane tips removed. Then, each succeeding winter all the canes produced in the current year were harvested, leaving only sufficient root in the ground to furnish the plot in the following season. By this system, fruiting, seeding and the formation of perennial root-stem systems (stooling) was prevented, thus ensuring a uniform supply of freshly rooted Mosaic-free canes. They were free also from Anthracnose (Cane Spot), Spur Blight and Cane Blight. These propagating

plots, and other plots of clonal origin built up later from single canes derived from them, supplied all the healthy indicator plants for the 1929 experiments and onwards, and, in addition, provided the basis for a system of Mosaic disease control for growers (13).*

With the establishment of such cane nurseries it was no longer necessary or practicable to provide individual clonal control plants for each indicator. An adequate proportion of each batch of indicator plants was, however, reserved for controls. Such plants were either left ungrafted or were grafted with scions from their own canes $\left(\frac{H}{H}\right)$. In all the experiments made up to the present the development of Mosaic symptoms on such control plants has occurred extremely rarely, a satisfactory check on the methods of propagation and greenhouse manipulation practised.

Infector plants.

Field plots for the isolation and propagation of selected Mosaic-affected stools were established from 1924 onwards. The produce of these plots was planted in pots where necessary (i.e. for cleft grafting and inarching), but when patch grafting was used, scion-canes were frequently cut directly from these plots or from affected plants in other plantations.

Methods of Grafting.

The main requirements of a method of grafting suitable for large scale symptom analyses on species and varieties of Rubus are:—

(i) rapid and easy manipulation ;
(ii) minimum of equipment and post grafting manipulation ;
(iii) reliability, i.e. a high proportion of successful unions ;
(iv) a long period in the season during which grafts can be made ;
(v) rapid development of symptoms on indicators ;
(vi) wide application, i.e. intervarietal and interspecific grafts possible.

Cleft grafting was found to be conspicuously deficient in respect of requirements (i) to (iii) and the following additional methods were therefore used.

1. Patch Grafting.

(a) *Ring method* (Text Fig. B and Plate I, Fig. 2).

This was first successfully applied to raspberries in the 1928 experiments, following closely the method used for black currants by Amos *et al.* (1) for the

* These and other experiments in commercial control have been made jointly with N. H. Grubb and a detailed account of them will be issued later.

transmission of Reversion. It has the advantage over cleft grafting that no frame or bell-jar protection is necessary and scion material is economized, i.e. several indicator plants can be graft infected from one short length of scion-cane.

A ring of the outer cane tissues (from epidermis to cambial layer) about $\frac{1}{2}$ in. wide was cut and peeled from an internode near the base of an actively growing new cane of the infector plant. A corresponding ring was then removed from a comparable cane of the indicator. The latter, however, was not completely ringed, but an isthmus about $\frac{1}{8}$ in. across was left intact. The scion-ring of cane tissue was then trimmed accurately to fit the depression in the stock-cane, with the vertical sides of the ring fitting closely against those of the isthmus. It was then tied firmly in position with a strip of Raphia bast, and thereafter re-tied at intervals to prevent constriction, until callusing was complete, generally about one month after grafting.

(b) *Panel method* (Text Fig. C and Plate I, Figs. 3 and 4).

This modification of the ring method is more easily and rapidly done, avoids severe mechanical weakening of the grafted cane, and minimizes the risk of constriction. After a successful trial in the 1932 experiment, it became the standard method in experiments at St. Catharines and thereafter at East Malling until replaced by the superior inarching method in 1937. It was also adopted by Chamberlain (6) at St. Catharines in his recent identification of Yellow-blotch Curl.

Instead of a ring, a small panel of the bark tissues about $\frac{1}{2}$ in. $\times \frac{1}{8}$ in. (the size of the isthmus left with the ring method) is cut and removed from the stock-cane and a similar panel from the scion-cane is substituted.

In the St. Catharines experiments in 1933-34 and thereafter, the grafts were secured by $\frac{3}{16}$ in. strips cut from a proprietary pure crêpe rubber bandage. This material is elastic, spongy and self-adhesive (but non-sticky), and a graft can therefore be sealed effectively by pressing the free end of the strip on to the strip itself. A disadvantage of this binding material, however, is its rapid deterioration on prolonged exposure to sunlight under warm summer conditions. Chamberlain at St. Catharines found it necessary to protect his graft "panels" from the liquefying rubber by an inner covering of waxed paper.

Grafting by this method was further accelerated by the use of razor-blade knives specially designed for the purpose by W. A. Roach. A full specification of these knives has been published (20).

Patch grafting is an improvement on cleft grafting in respect of points (i) to (iii). The proportion of failures by the former method, however, although lower on the whole than by the latter was still considerable.

This method moreover has the following disadvantages with regard to requirements (iv) to (vi).

(iv) The grafting period for plants under pot culture is very restricted.

(v) The transmission of leaf symptoms to the indicator is, under East Malling conditions, generally delayed until the season following that of grafting (some 10-12 months).

(vi) Considerable incompatibility in inter-varietal grafts of red raspberry has been experienced (conspicuously with the variety Lloyd George) and interspecific cross grafts of Rubus have so far failed.

(c) *"Inarching"* (Text Fig. D and Plate I, Fig. 5).

This method was first used successfully in 1937 but after limited experience appears to fulfil all the above requirements. In that year, 43 of the 45 grafts were successful. They included the following:—

(a) All combinations of selected European and American varieties of red raspberry and American black raspberry (*R. occidentalis*).

(b) All combinations of loganberry and phenomenal berry.

(c) European red raspberry and phenomenal berry grafted to cultivated varieties of blackberry.

Plants ill-matched in vigour, including diseased specimens with dwarf, stunted canes and bines of small diameter (quite unsuitable for grafting by the previous methods) were successfully inarched, at all times when the canes and bines were elongating.

On the other hand this method requires more greenhouse space and material than the previous ones. The infector plants must be grown in pots and must be contiguous to the indicator plants for at least three months. It is of course possible to inarch as many indicator plants with one infector plant as there are suitable canes or bines on the latter and as space around it permits.

Inarching can readily be effected in the open plantation, and indicator plants in pots have temporarily been plunged side by side with stools in field plantations for this purpose, to be removed later with a portion of the inarched infector cane when union had been effected.

The procedure is very similar to that of the previously described stolon inarching of strawberry plants (13). A diagonal cut about 1 in. in length and extending from the circumference to the axis of the stem is made in opposite directions in the growing apical region of a cane (or bine) on the indicator and infector plants. The resulting tongues are then engaged as shown in Text Fig. D, and the region of insertion is sealed by wrapping around it a rectangular piece of crêpe rubber bandage and pressing the junction edges together until the graft is

tightly secured. The superfluous bandage ends are then removed or folded over to afford additional support, and the whole union is covered with a wrapping of tin-foil to protect the rubber from the sun. Finally, the inarched canes are tied together with rubber or Raphia bast below and (if necessary) above the graft and the whole tied to a stake. After grafting, the units are carefully watched, and adjustments in the ties and supports are made from time to time to avoid strain due to the often unequal elongation of the inarched canes. When union had occurred (in most cases within 3 to 4 months after grafting) the indicator plant was detached from the infector by severing the inarched infector cane below the union, thus leaving the top of the latter grafted to the indicator plant.

THE ETIOLOGICAL RELATION OF SYMPTOM TYPES *a*, *b* AND *c*.

The first experiments in analysis consisted of parallel transmissions to normal Baumforth's Seedling B indicators from infectors selected as showing each of the three symptom types (11) uncomplicated with the other two.

Three infector varieties were selected, Baumforth's B for types *b* and *c*, Mitchell's Seedling for type *a* and ?*c*,* and Norwich Market as another representative of the high susceptibility group, but, unlike the two other varieties, affected with uniformly severe symptoms of indeterminate type.

The infector canes of Baumforth's B with symptom type *c* were taken from the Mosaic-affected stools on isolation plot 1, showing a uniformly mild infection (see 11, page 244 and Plate III, Fig. 1). The vigour of these stocks did not differ appreciably from that of the corresponding healthy stools. Infector canes of this variety with symptom type *b* were taken from the affected stock plants of the previous (1926-27) experiments.

The infector canes of Mitchell's Seedling were collected directly from stools in the Research Station variety plots. Each stool, at this time, exhibited either one or the other type of symptom. Stunting and lack of vigour was most severe on stools showing type *c* symptoms.

The infector canes of Norwich Market were taken at random directly from the variety collection in which all the stools were equally stunted and completely unproductive.

A clonal control plant was provided for each graft-inoculated plant and both cleft grafting and patch grafting were used.

Detailed records of symptom development and plant vigour (including cane length measurements) were made regularly for the three consecutive seasons after grafting.

Results. The results are summarized in Table II and illustrated in Plate III, Figs. 1 and 2.

* Severe symptoms resembling type *c* ((11) Plate I).

TABLE II.

Symptom Analysis of Baumforth's Seedling B, Mitchell's Seedling and Norwich Market.

Infector.		Indicator Variety.	Year of Graft.	Successful Unions.	Analysis of Records on Indicator Plants.						
					Leaf Symptoms.			Rate of Decline.			
Variety.	Symptom type.				Type *b*	Type *c*	Types *b* and *c*	Nil to slight.	Moderate	Rapid.	Drastic.†
BB*	*b*	BB*	1926	12	7	—	5	7	—	5	—
	b	BB	1928	2	2	—	—	2	—	—	—
BB	*c*	BB	1928	9	—	9	—	5	4	—	—
Mitchell's Seedling	*a*	BB	1928	4	—	4	—	2	—	1	1
	?*c*	BB	1928	5	—	5	—	—	—	4	1
	?*c*	BB	1930	1	—	1	—	—	1	—	—
Norwich Market ..	?	BB	1928	2	—	2	—	—	—	—	2

* Baumforth's Seedling B. † Dead within one year.

BAUMFORTH'S SEEDLING B.

In 18 of the 23 units in which successful union occurred the symptom type selected (*b* or *c*) was transmitted unchanged to the indicators within a period of 2 to 12 months (depending on the method of grafting). With one exception, the indicators thus infected and the infector plants (in pots) remained true to the symptom type over the three-year period. The exception was a plant infected with type *c* symptoms in 1928 which developed combined type *b* and *c* symptoms in 1930. As the infector remained true to type and the control healthy this was probably due to an additional infection from an extraneous source.

In their general reaction to infection, the indicators grafted with infectors showing symptom type *b* showed pronounced uniformity. Leaf symptoms of this type were transmitted with marked regularity, and, on comparing infected plants with controls these symptoms were associated with a uniformly slow decline in plant vigour from year to year.

With symptom type *c*, the reaction was irregular. In two cases very transitory and slight leaf symptoms were detected on one or two leaves in the year following grafting, but thereafter no symptoms were observed. These plants showed no appreciable decline in vigour when compared with the control plants. The symptoms on the remaining plants were more intense and were distributed over the whole plant. All these plants declined perceptibly in vigour, but some very slowly and others with moderate rapidity. The parallel observations on the naturally affected infector plants corresponded closely to those on the graft infected plants.

MITCHELL'S SEEDLING.

From Table II it will be seen that type *c* symptoms were transmitted to the Baumforth's B indicators alike from type *a* infectors and from infectors showing the intense symptoms provisionally classified as type *c*. The symptoms transmitted, however, although qualitatively identical varied considerably in intensity. Thus, the type *c* infectors induced a moderately rapid to drastic decline of the indicators, two plants dying the year following that of infection (Plate III, Figs. 1 and 2). Two of the type *a* infectors caused a similarly drastic reaction, but in the two remaining transmissions the reaction was extremely mild, with sparse leaf symptoms.

Parallel observations for three years on naturally infected Mitchell's Seedling plants in pots provided the following supplementary data. Two of the four plants selected as showing type *a* symptoms retained these symptoms and a moderate standard of vigour throughout the period. The remaining two plants rapidly developed the intense type of symptoms shortly after transplanting, and

rapidly declined in vigour, one plant dying within a year of transplanting. During this transition from the type *a* to type *c* condition, leaves with each symptom type occurred simultaneously on the same plant. In contrast to the type *a* plants, all the type *c* plants consistently exhibited intense symptoms of this type after transfer to pots, and all declined rapidly in vigour. Occasional leaves with type *a* symptoms were, however, observed on two of these plants.

From the above observations the anomalous reaction of the indicators to the type *a* infection may be interpreted as due to the inadvertent selection of some infector canes from plants already developing the severe condition. (See Discussion below.)

Norwich Market.

Owing to the generally degenerate condition of cane growth of this variety, the majority of the grafts on Baumforth's B failed. In the successful unions, however, type *c* symptoms were transmitted. The intensity of these symptoms was extremely high in both cases ; the indicator plants rapidly declined and died within the year following grafting. All the controls remained vigorous and healthy.

Discussion.

The above results show that the range of Mosaic leaf symptoms in the three raspberry varieties can be referred to two etiologically distinct disease groups, one represented by type *b* symptoms on Baumforth's B, the other by type *c* symptoms on the same variety, by types *a* and ?*c* symptoms on Mitchell's Seedling and by the indeterminate symptoms on Norwich Market.

It is proposed provisionally to refer to the former disease group as Mosaic 1 and the latter as Mosaic 2.

Mosaic 2 can be further divided into two sub-groups, (i) *Mild Mosaic 2* with slight and evanescent type *c* leaf symptoms (type *a* on Mitchell's Seedling) and undetectable or very slow decline of the indicator ; (ii) *Severe Mosaic 2* with intense and concentrated type *c* leaf symptoms and a rapid decline and death of the indicator.

In the above experiments Mild Mosaic 2 was transmitted by some of the Mitchell's Seedling type *a* infectors and by all the Baumforth's B type *c* infectors. Severe Mosaic 2 was transmitted by the remaining type *a*, and all the type ?*c* Mitchell's Seedling infectors and by Norwich Market. It must here be noted that natural infections with Severe Mosaic 2 were found in field plantations of Baumforth's B during the experiments. The use of such weak stools as infectors, however, was not possible by patch grafting methods but was made readily possible by the more recently employed inarching method.

The possible relationships of Mild and Severe Mosaic 2 may be considered to be as follows:—

(1) Phases of a single virus disease due primarily and entirely to variation in local environmental or cultural conditions.

(2) Due to mild and severe strains of one virus with mutually protective action.

(3) Caused by distinct and independent viruses.

(4) The result of two or more interacting viruses, i.e. Severe Mosaic 2 induced by the interaction of the virus of Mild Mosaic 2 and another (activating) virus.

The above considerations imply an etiological distinction between Mild and Severe Mosaic 2 and therefore eliminate assumption No. 1 as a complete explanation of the observed changes from the mild to the severe condition. If No. 2 (multiple virus strains) is postulated, this transition may be interpreted as primarily due to the reversal of a mutually competitive (or "protective") relationship between mild and severe virus strains jointly occupying the affected plants. In the promotion of such a dominance of severe strains environmental changes might well play an important part, and a possible instance is provided by the rapid passage of the symptoms in Mitchell's Seedling variety to the severe condition on transfer to East Malling from its native Scottish habitat.

The available facts however may alternatively be interpreted by assumptions (3) or (4), implying that mildly affected plants pass to the severe condition on infection by an independent virus or by an activating virus, respectively. Such explanations, however, do not readily account for the above rapid and widespread development of the severe condition in Mitchell's Seedling on its removal to a new environment. Further data are necessary to reach a final decision, but meanwhile, on the basis of the qualitative identity of the leaf symptoms on Baumforth's B, both categories will be provisionally retained as sub-groups of Mosaic 2.

ANALYSIS OF SYMPTOMS IN LLOYD GEORGE AND RED CROSS VARIETIES.

Lloyd George.

At the time of the present experiments the variety Lloyd George, owing to its exceptionally high qualities of adaptation, vigour and yield, had become (and still remains) the dominant commercial variety of raspberry throughout the British Isles. Early field observations indicating an apparent marked susceptibility to Mosaic have been summarized elsewhere (11). In 1928 an analysis of symptoms by experiment was started in order to provide data for

a system of field-control by roguing (14) and to determine its usefulness as an additional indicator variety, Baumforth's Seedling B having proved far from satisfactory owing to its weak cane habit. In the field, the leaf symptoms were clearly not homogenous but there was no clear-cut distinction of type comparable to the symptoms seen in Baumforth's B and Mitchell's Seedling. A distinction between two symptom groups, roughly analogous to types *b* and *c*, was, however, made in the selection of infector canes for the early experiments. Type *b* included leaves with laminae symmetrically down-curled about the mid-rib and a light even mottling tending to concentrate towards the leaf-margins (Plate IV, Fig. 1). Type *c* showed an irregular laminal distortion with irregularly shaped and distributed, deeply depressed, chlorotic areas (Plate IV, Fig. 2).

The results are summarized in Table III.

(1) No symptoms were detected on Lloyd George artificially infected by Mild Mosaic 2 derived from both Baumforth's B and Mitchell's Seedling. The corresponding decline in vigour was uniformly so slight as to be indeterminate. That the variety was actually a symptomless carrier of Mild Mosaic 2 followed from the transmission of this disease from naturally infected canes. (See (3) below.)*

(2) The provisional field identification of type *b* (Mosaic 1) symptoms on this variety was confirmed.

(3) Combined infection with Mosaics 1 and 2 was shown to occur naturally on Lloyd George and the symptoms of the joint attack differed considerably from those of Mosaic 1 alone, i.e. type *b* symptoms (Plate IV). Before the analysis these joint symptoms were provisionally classified as type *c* (Mosaic 2).

(4) The moderate to rapid decline of two of the Lloyd George indicators after the transmission to them of Mosaic 1 from Baumforth's B is interpreted as being due to a previous masked infection of these indicator plants with Mosaic 2.

The reaction of Lloyd George to Severe Mosaic 2 was later determined by the experiments with the Red Cross variety, and consideration of the general conclusions from the above analysis will therefore be deferred until after the description of those experiments.

RED CROSS.

The variety Red Cross was selected for early analysis because of its hitherto unique reaction to Mosaic disease (11). All stools examined from 1922 onwards have been affected with the disease, but no corresponding signs of a general

* Further experimental evidence on this point is being procured by inarching Baumforth's B to Lloyd George indicators.

TABLE III.

Analysis of Varieties Lloyd George (L.G.) and Red Cross (R.X.).

Infector plant.		Indicator plant.	Year of Graft.	Successful Unions.	Analysis of Records on Indicator Plants.								
					Leaf Symptoms.					Rate of Decline.			
Variety.	Symptom type.	Variety.			Nil.	Indeterminate.	Type *b*	Type *c*	Types *b* and *c*	Nil to slight.	Moderate.	Rapid.	Drastic.†
L.G.	?	B.B.	1930	2	—	1	—	—	1	—	—	1	1
L.G.	?*b*	B.B.	1932	1	—	—	1	—	—	1	—	—	—
L.G.	?*b*	L.G.	1932	2	—	—	2	—	—	2	—	—	—
L.G.	?*c*	B.B.	1932	4	—	—	—	—	4	2	1	1	—
L.G.	?*c*	L.G.	1932	1	—	1	—	—	—	—	1	—	—
B.B.	*b*(M.1)*	L.G.	1930 1932	5	—	—	3	—	2	3	1	1	—
B.B.	*c* (M.2 mild)	L.G.	1930 1932	7	7	—	—	—	—	7	—	—	—
Mit. S.	*a*(M.2 mild)	L.G.	1928 1930	4	4	—	—	—	—	4	—	—	—
R.X.	?	B.B.	1932	10	—	—	—	10	—	—	—	10	—
	?	B.B.	1937	2	—	—	—	2	—	—	—	—	2
	?	L.G.	1937	5	5	—	—	—	—	—	—	5	—

* Mosaic 1.

† Dead within one year.

decline in vigour of the variety have been detected up to the present. It still occupies a place among the uniformly highest cropping varieties on the Research Station plots (10). With apparently complete infection and uniformly high resistance to deterioration the value of the variety as a reliable source of one (or more) of the Mosaic diseases in routine analyses and tests was early recognized, and the first graft combinations with Baumforth's B and Lloyd George indicators, to determine its precise disease group (or groups) were made in 1930 by the ring patch grafting method. The results of this experiment were inconclusive. All the grafts on Lloyd George indicators failed to make union and only two of the RX/BB combination were successful. The Baumforth's B indicator of one of the latter units later developed severe leaf symptoms somewhat similar to those of type *b*, but at the same time its clonal control plant developed suspicious symptoms. On the indicator of the other unit no leaf symptoms were recorded but the plant was dead in the spring of 1931. One further Baumforth's B indicator in the series developed type *b* leaf symptoms in 1931, but as the graft was a failure this is ascribed to extraneous infection. A further attempt was made in 1932 by the panel patch grafting method. Again all the grafts to Lloyd George failed, but ten combinations with Baumforth's B were successful. (See Table III.) Each of these indicators developed uniformly severe type *c* symptoms.

Finally, in 1937, using the inarching method, two further RX/BB combinations and a series of five combinations with Lloyd George indicators resulted in successful union. The results from the former units were identical with those of the 1932 series, for severe Mosaic 2 symptoms were induced in each indicator. Each of the RX/LG units reacted uniformly ; no leaf symptoms were detected on the indicators, but a rapid decline in vigour took place after grafting ; each of the vigorous Red Cross infectors also declined, and died the year following grafting.

Discussion.

The above data confirm the etiological distinction of the two groups of Mosaic disease, i.e. Mosaic 1 and Mosaic 2, and indicate a multiple virus origin for the severer diseases in Group 2. The uniformly affected Red Cross variety grafted to Baumforth's B indicators was found to be affected solely with Severe Mosaic 2. Lloyd George, on the other hand, proved to be affected with Mosaics 1 and 2, to each of which diseases it reacted in very different manner.

Thus, the reaction of Lloyd George to Mosaic 1 was closely similar in leaf symptoms and other respects to that of Baumforth's B. In contrast, no leaf symptoms were expressed by Mosaic 2 (Mild or Severe).* The observed

* This disease, however, modified and greatly intensified the symptoms of Mosaic 1 in cases of joint infection.

reaction of the mild disease on plant vigour was, also, so slight as to be inappreciable, and it is clear from certain anomalous results that some of the apparently normal Lloyd George indicators were already affected with Mosaic 2 before the experiments started. The decline of both Lloyd George indicators and Red Cross infectors after inarching must be interpreted as a reciprocal effect of a further interaction of Mosaic 2 viruses from the latter or both varieties.*

ANALYSIS OF OTHER VARIETIES.

The limited data at present available on varieties other than those dealt with above are summarized in Table IV. The absence of any Mosaic 1

TABLE IV.

Data on Miscellaneous Varieties.

Variety.	Baumforth's B.		Lloyd George.	
	Successful Unions.	Reaction.	Successful Unions.	Reaction.
Bath's Perfection	2	Severe Mosaic 2	—	—
Red Magnum Bonum ..	1	Severe Mosaic 2	—	—
Reader's Perfection ..	1	Mild Mosaic 2	—	—
Baumforth's A	4	Severe Mosaic 2	2	Mosaic 2
Maclaren's Prolific ..	1	Mild Mosaic 2	—	—
Preussen	—	—	1	Mosaic 2

reaction must not be interpreted as indicating the non-incidence of this disease on the listed varieties. Reader's Perfection, for instance, in its reaction to Mosaic disease (as in its horticultural characters) closely resembles Baumforth's B in exhibiting both type *b* and type *c* symptoms. Baumforth's A and Maclaren's Prolific are varieties previously classified (on field observations) as of low infectibility and low susceptibility (11). As a result of the present tests, the susceptibility of Baumforth's A to Severe Mosaic 2 must now be regarded as at least moderate. Bearing in mind the tendency of Mosaic 2 (particularly Mild Mosaic 2) to symptom suppression, it is extremely probable that the low infectibility of these varieties may be apparent only, i.e. that they may be symptomless carriers. This possibility also applies to Bath's Perfection and to Preussen. The former is an introduction from North America (syn. "Marlborough") and was widely grown and a heavy cropper during the Great War. Since then it has rapidly dropped out of cultivation, and observation has shown that the existing stocks are in a generally deteriorated condition.

* On the hypothesis of multiple virus strains (p. 335) this would imply the breakdown of a protective dominance of mild over severe strains, resulting in increased action of the latter in both the inarched varieties.

Symptoms of Mosaic on this variety are very indistinct, and it is only when stools are closely examined that a wide distribution of symptoms becomes evident. The variety is now regarded as completely infected with Mosaic 2.

Similar observations have recently been made on Preussen. Stools which on cursory examination appear to be normal commonly show a slight mottling on one or two apical leaves only. The reaction to Mosaic 2 in such varieties as the above is thus seen to correspond closely with that in Lloyd George, and it is therefore concluded that the incidence and reaction of this disease is wider and more serious than can be deduced from the incidence of leaf symptoms alone. Final conclusions on this point must await further and more extensive grafting tests which are now in progress.

GENERAL DISCUSSION AND CONCLUSIONS.

In the above experiments Mosaic disease was transmitted by grafting from nine varieties of European red raspberry and one variety of American origin (Bath's Perfection) to the European variety Baumforth's B, and in each case one of two sharply differentiated qualitative types of leaf symptom (types *b* and *c*) or a combination of these types was consistently induced. On this basis the symptoms of Mosaic disease of the European red raspberry are provisionally referred to two etiologically distinct groups, Mosaic 1 and Mosaic 2, the principal distinguishing features of which are as follows:—

Mosaic 1. On Baumforth's Seedling B the symptom expression is uniformly mild, irrespective of the variety from which infection is derived. The distinctive leaf symptoms, type *b* (11), are generally exhibited by all canes of an affected stool with marked regularity, masking occurring only under hot midsummer conditions. Its expression on the other two varieties on which it has been identified, Lloyd George and Reader's Perfection, closely resembles in leaf symptoms and all other respects that on Baumforth's B. The above features of Mosaic 1 are those of a simple disease, probably of single virus origin, uniformly mild in character and of comparatively restricted varietal distribution.

Mosaic 2 comprises two or more diseases of differing intensity, from mild to very severe, but inducing the qualitatively identical and distinctive leaf symptoms on Baumforth's Seedling B described as type *c* (11). Severe Mosaic 2 has been transmitted to this variety from eight European varieties in addition to itself, and from one variety of American origin (Bath's Perfection). These varieties were found to vary greatly in their susceptibility to the diseases of this group. Thus, stools of Baumforth's B were rapidly rendered completely unproductive by infection from the highly resistant Red Cross. Another distinctive feature common to both Mild and Severe Mosaic 2 is a tendency to the masking or irregular expression of leaf symptoms. Thus, in experiments

so far made, Lloyd George has reacted as a symptomless carrier of Mosaic 2, although the vigour of infected stools appears to be reduced by the severer diseases of the group. Again, the symptoms of Mild Mosaic 2 on Baumforth's B and of Severe Mosaic 2 on resistant varieties such as Preussen or Red Cross, may be suppressed for a season or so, or may be limited to the leaves of one or two canes or to a single leaf. There is also considerable divergence of the actual form of the leaf symptoms from the type *c* of the indicator Baumforth's B, e.g. the type *a* and type ?*c* of Mitchell's Seedling, and the leaf symptoms of Red Cross differ in many respects from the symptoms of Mild and Severe Mosaic 2 on the indicator variety. No masking of symptoms of Mosaic 2 by high summer temperatures has been observed.

The above are the principal grounds on which Mosaic 1 and Mosaic 2 are finally distinguished. The grouping of the Mosaic 2 diseases, however, being based at present mainly on striking analogies of symptoms must be regarded as provisional, pending a final determination of their precise relationship.

Finally, the striking parallel between Mosaic 1 and Mosaic 2 and the American Yellow Mosaic and Green Mottle Mosaic must be noted, in particular the similarity between the last named, with its mild and severe forms, and Mosaic 2. Further discussion of this important point is deferred pending the completion of experiments in the direct comparison of the European and American diseases.

ACKNOWLEDGMENTS.

The writer is especially indebted to Dr. H. Wormald for his interest, advice and help at all stages of the work ; to Mr. N. H. Grubb for invaluable collaboration throughout ; to Mr. A. W. Witt for help and suggestions in the grafting operations ; to Dr. W. A. Roach for the grafting knives ; to Mr. A. Tidy for his expert care of the plant material ; and to Miss M. E. King for the text figure.

SUMMARY.

1. All experiments in the transmission of raspberry Mosaic by mechanical means have given negative results.

2. Initial attempts in 1926-27 to transmit Mosaic symptoms to normal plants of the variety Baumforth's Seedling B by grafting yielded positive results, indicating the virus origin of the disease.

3. Successful methods of transmission by cleft grafting, patch grafting and cane inarching are described.

4. Experimental work carried out from 1928-37 on the analysis of the range of symptoms in some ten varieties of red raspberry by grafting is described.

5. On the results of the experiments the symptoms are referred provisionally to two distinct etiological categories, Mosaic 1 and Mosaic 2.

6. Mosaic 1 expresses type *b* symptoms on the indicator variety Baumforth's B, behaves as a single disease, probably of single virus origin, is uniformly mild in expression and of comparatively limited varietal distribution.

7. Mosaic 2 includes diseases expressing type *c* symptoms on Baumforth's B, but differing in intensity of expression from mild to extremely severe.

8. Mosaic 2 is widely distributed among local varieties and these show a wide range of susceptibility to injury. Red Cross is totally infected but highly resistant, with an irregular expression of distinct leaf symptoms. No leaf symptoms have yet been expressed on artificially infected Lloyd George plants. Stools of susceptibles, e.g. Baumforth's B and Mitchell's Seedling, are rapidly rendered unproductive by Severe Mosaic 2 and die.

9. Combined infection with Mosaic 1 and Mosaic 2 has frequently been identified. The severe economic form of Mosaic in Lloyd George consists of such joint infection.

REFERENCES.

(1) *Amos, J., Hatton, R. G., Knight, R. C.* and *Massee, A. M.* "Reversion" in black currants. Its causes and eradication. E. Malling Res. Sta. Ann. Rept. 1927 (1928), 43.

(2) *Bennett, C. W.* Virus diseases of raspberries. Michigan State Agric. Expt. Sta. Tech. Bull. 80, 1927.

(3) ———. Further observations and experiments on the curl disease of raspberries. Phytopath., 1930, **20**, 787.

(4) ———. Further observations and experiments with mosaic diseases of raspberries, blackberries and dewberries. Michigan State Agric. Expt. Sta. Tech. Bull. 125, 1932.

(5) *Blattný, C.* O. virisoých chorobách Malinniku a Ostruźinníku. Ochrana Rostlin, 1927, **7**, 62.

(6) *Chamberlain, G. C.* Yellow Blotch-Curl: A new virus disease of the red raspberry in Ontario. Can. Journ. Res. C., 1938, **16**, 118.

(7) *Cooley, L. M.* The identity of raspberry mosaics. Phytopath., 1936, **26**, 44.

(8) *Dickson, B. T.* Studies concerning mosaic diseases. Macdonald College, Canada. Tech. Bull. 2, 1922.

(9) *Grainger, J.* and *Angood, E.* The insect transmission of raspberry mosaic. Proc. Leeds Phil. & Lit. Soc. (Scient. Sect.), ii, 1931, **4**, 183.

PLATE I.

FIG. 1. A successful cleft graft.

BB
BB

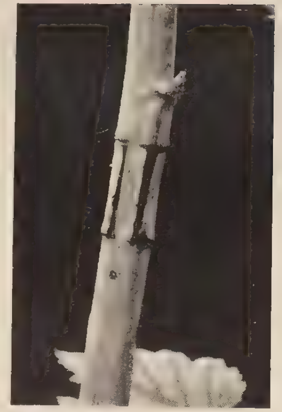


FIG. 2. A patch graft. Ring method.

FIG. 3. A patch graft. Panel method with crêpe rubber binding.

FIG. 4. As Fig. 3, but further advanced; well callused.

FIG. 5. An inarch union well callused.

PLATE II.

Fig. 1. Normal Baumforth's B cleft grafted with Mosaic-affected Baumforth's B $\left(\frac{M}{H}\right)$. Symptom types *b* and *c*.

Fig. 2. Control to the above. $\left(\frac{H}{H}\right)$

1927 Grafting Experiment. Grafts made 12/5/27. Photos, June 1928.

PLATE III.

FIG. 1. Baumforth's B patch grafted (ring) with Mitchell's Seedling type ?c. (Severe Mosaic 2.) Type *c* symptoms developing. Graft, 15/6/28. Photo, 20/6/29. This plant died later in 1929.

FIG. 2. Another plant grafted as in Fig. 1. Type *c* symptoms.

FIG. 3. Lloyd George cleft grafted with Mitchell's Seedling type *a* (Mild Mosaic 2). Symptoms on latter (scion), none on former (stock). Graft, 6/7/28. Photo, 16/5/29.

PLATE IV.

FIG. 1. Lloyd George graft-infected with Mosaic 1 (type *b* symptoms).

FIG. 2. A Lloyd George new cane with combined natural infection with Mosaic 1 and Mosaic 2.

(10) *Grubb, N. H.* The cropping of raspberry varieties at East Malling. E. Malling Res. Sta. Ann. Rept., Supplement 1928-30 (1931), 32.

(11) *Harris, R. V.* Mosaic disease of the raspberry in Great Britain. I. Symptoms and varietal susceptibility. Journ. Pom. & Hort. Sci., 1933, **11**, 237.

(12) ———. Some observations on the raspberry diseases situation in North America. E. Malling Res. Sta. Ann. Rept. 1934 (1935), 156.

(13) ———. Grafting as a method of investigating a possible virus disease of the strawberry. Journ. Pom. & Hort. Sci., 1932, **10**, 35.

(14) ——— and *Grubb, N. H.* The commercial control of raspberry mosaic. E. Malling Res. Sta. Ann. Rept. 1932 (1933), 149.

(15) *Rankin, W. H.* and *Hockey, J. F.* Mosaic and Leaf Curl of the cultivated red raspberry. Canad. Dept. Agric. Div. Bot. Dom. Expt. Farms, Circ. No. 1 (N.S.), 1922.

(16) ——— and ———. Mosaic and Leaf Curl (Yellow) of the cultivated red raspberry. Phytopath., 1922, **12**, 253.

(17) *Rankin, W. H.* Mosaic of raspberries. N.Y. State Agric. Expt. Sta., Geneva, Bull. 543, 1927.

(18) ———. Probable identity of red and mild mosaic of black raspberries. Phytopath., 1930, **20**, 125.

(19) ———. Virus diseases of black raspberries. N.Y. State Agric. Expt. Sta., Geneva, Tech. Bull. 175, 1931.

(20) *Roach, W. A.* Budding and grafting razors. Gard. Chron., 1934, **96**, 196.

(21) *Wilcox, R. B.* and *Floyd Smith, F.* Transfer of mosaic disease from red to black raspberries. Phytopath., 1924, **14**, 55.

(*Received* 29/9/39.)

WATER-CULTURE STUDIES WITH APPLE TREES—II

THE SEASONAL ABSORPTION OF NITROGEN AND POTASSIUM BY COX'S ORANGE PIPPIN ON MALLING ROOTSTOCKS NOS. IX AND XII

By H. L. PEARSE

Research Institute of Plant Physiology, Imperial College of Science and Technology, and East Malling Research Station

INTRODUCTION.

Hatton and Grubb (10) first drew attention to the fact that trees on certain rootstocks of the Doucin types—particularly those on No. V—were very susceptible to the physiological trouble commonly known as Leaf Scorch. Hatton (11) has pointed out that the work of Wallace (26, 27), which showed that this disorder was correlated with potassium deficiency, suggests the possibility of a differential response of a single variety upon different rootstocks to a similar nutritional treatment. Warne and Wallace (28) investigated the possible relationship between rootstock effect and chemical composition of the shoots of the scion; two scion varieties, Worcester Pearmain and Lane's Prince Albert, worked on a number of different vegetatively propagated rootstocks, were used, and chemical determinations were carried out on terminal shoots collected during July. They found that shoots on rootstocks Malling II and V, which often bear scorched foliage, were low in potash, even under conditions of favourable potash supply; rootstocks promoting great vigour in the scions showed agreement in respect of only one character, viz. a high K/N ration in the shoots; but it was not found possible to explain the dwarfing effect of Malling IX rootstock on the basis of any chemical feature.

The results in general showed that although the rootstocks produced significant differences in certain chemical constituents of the terminal shoots of both varieties, many of the outstanding rootstock effects could not be explained on the basis of the chemical characters examined.

Vaidya (23) has recently investigated throughout the season the mineral and nitrogen content of shoots of scions worked on various Malling clonal rootstocks, and has shown many interesting differences in the seasonal cycles. Such studies, however, give a picture of the chemical content of the shoots only under the soil conditions prevailing during the experimental period. They give little information about the relative absorption capacity of the roots of the

various rootstocks, since it is well known that one of the chief factors affecting absorption is the concentration of the soil solution in contact with the roots. Thus, a light shower of rain might affect the absorption rate of a surface rooted tree in a manner entirely different from that of a deeply rooted one. Again, Chandler (6) has shown that with high potash manuring it is possible for apple trees to contain very much more potash than similar trees not manured with potash, without this higher content in the manured trees having any measurable effect on their growth.

Accordingly, the present work was started to study the seasonal absorption of the chief nutrient ions, N, P and K, by trees worked on various clonal root-stocks, and to determine if there are marked differences between these rootstocks in respect of (1) the time of maximum absorption of the various nutrient ions; (2) the total amounts absorbed; and (3) the relative amounts of the various ions absorbed. It has already been pointed out that for experiments of this type it is an obvious advantage if the concentration of the nutrients actually in contact with the absorbing surfaces of the roots is maintained as constant as possible. One of the best ways of achieving this is by the method of water-culture, for with it the concentration of the solution in contact with the absorbing roots does remain practically constant, provided the solution is frequently changed. This method was therefore selected.

REVIEW OF THE LITERATURE.

Growth of Trees in Water-Culture.—Although comparatively little work has been done with trees growing in solutions of salts, yet water-culture work with plants really began with the growing of trees in water. Duhamel du Monceau (9) described the growth of almond, oak and chestnut trees in the water of a fountain in a garden in France. The fountain was supplied with water from the river Seine, and an oak tree that arose apparently from an acorn accidentally dropped into the fountain, grew for some eight years with no other mineral nourishment than that supplied by the water in the fountain. At the end of this time the "tree" was 18 in. high. An almond tree grew well for four years in the same fountain, and the chestnut tree apparently grew as well in water as in soil and was transplanted to garden soil after two years in the fountain. Duhamel was convinced that only water was needed for plant growth, not realizing that the river water in the fountain carried salts in solution. His experiments and conclusions widely influenced the views on plant nutrition at that time and, in fact, until de Saussure, in 1804, finally corrected the error by growing plants in distilled water with and without added salts.

Much later Wolff and Knop (30) grew oak trees in solutions of salts up to an age of fifteen years, and this probably still stands as a long time record for such work. These investigators placed their trees in river water during each

winter, and at the end of fifteen years the trees were approximately 1·6 metres high and the stem circumference was about 5 cm. Fifteen-year-old forest oak trees were 8-9 metres high with a stem circumference of 30·4 cm.

Nobbe (16) had fair success with two-year-old elm trees in water-culture, and found that the ash content of these trees was usually greater than that of trees grown in soil. Bain (1) grew peach and apple seedlings and grape vines in salt solutions and studied the sensitivity of the roots to copper in solution. Apple roots were found to be most sensitive, peach less so, and grape least sensitive. Reed and Haas (19) made use of water-cultures in studying the nutrition of young Citrus seedlings. Combes (8) compared the chemical composition of beech trees grown in water-culture with that of similar trees grown in forest soil, and Colby (7), who studied the effects of a deficiency of particular elements on the seasonal and total nitrate absorption of French prune trees grown in water-culture, found that potassium, magnesium and phosphorus starvation all depressed nitrogen absorption very seriously.

Nutritional and Seasonal Absorption Studies with Fruit and Forest Trees.— General nutrition studies on Citrus have been made by Reed and Haas (19), and others on apple, plum and small fruits by Mann (15) and Wallace (24, 25, 26, 27).

Such knowledge of the nutrition of deciduous fruit trees as exists has not come from water-culture work, but from sand-cultures or from field manurial experiments which have been carried out in various parts of the world for many years. Naturally the results from the latter type of experiment are often difficult to interpret because of the complicated soil conditions. The most light has been thrown on the nutrition of trees through sand-culture methods aided by chemical analyses of the tissues of trees grown in this way under various nutritional conditions.

In the sphere of sand-cultures of deciduous fruit trees the work of Wallace (24) is outstanding. He was chiefly interested in the effects of a deficiency of particular nutrients on young trees of apple and plum, and on strawberry and gooseberry among small fruits. Trees were starved of single elements over periods of three consecutive years, and differences were recorded in the ash content of the various organs after such starvation. He made no studies, however, of seasonal absorption with any of his plants or trees.

Roberts (20, 21) grew dwarf apple trees in sand-cultures with high and low amounts of nitrogen and under short and long day conditions, and he concluded that the type of growth of a tree is a response to the balance of carbohydrate/nitrogen content, rather than to the absolute amounts of these materials present in the tree.

In Germany, plant physiologists have made many detailed studies on seasonal absorption by forest trees, and they indicate the wide variation that

can occur in the course of absorption by different types of tree. Bauer (3, 4, 5) found that apparently every species of forest tree has a different course of mineral and salt absorption throughout the year, as well as a different curve of dry weight increase. Frequently, absorption and dry weight increase followed closely the same path, but this was not always so, and probably there is never perfect correlation between them ; moreover, the same tree may have very different seasonal absorption rates for various ions. Although nitrogen and potassium absorption curves usually run parallel, those for nitrogen and magnesium or for nitrogen and phosphorus may be very different. In the fir, absorption of nitrogen occurs before June each year, with little or no nitrogen absorption from June to September in most cases. The horse chestnut, on the other hand, took in nitrogen from June to November, continuing rapid absorption until very late in the autumn. Larch took up hardly any nitrogen in June but absorbed potassium, calcium, magnesium and phosphorus at that time. The maximum absorption rate of nitrogen in the ash tree was in June, and in the beech, in August. These studies show the considerable variation that can occur in the course of the seasonal absorption of nutrients with different species of trees.

METHODS.

(1) Cultural.

The water-culture method of growing apple trees was selected by the writer since, in addition to the advantage, already mentioned, of maintaining a reasonably constant nutritional environment for the roots, it has a number of distinct advantages over other methods of culture for studies in fruit tree physiology: (i) It allows of a comparatively easy and accurate study of absorption where only a small number of trees is used, the losses from the cultural solution being employed to determine the time and amount of absorption of the nutrient ions. With the alternative method, that of harvesting periodically a certain number of entire trees and analysing the ash of the whole tree each time, a great many trees must be used. In addition, undue time and labour are required for digging up the roots, careful washing, drying, grinding, weighing and ashing the tissues and analysing the ash. (ii) The roots are under continual observation. (iii) The fresh weight of the trees can be determined at any time with a moderate degree of accuracy. (iv) Factors such as soil variation and root competition are eliminated. (v) The difficulty of obtaining an entirely nutrient-free sand is overcome. Wallace (27), using sand-cultures, reported that " minus calcium " trees gave as good shoot growth as did " complete culture " trees ; and he states that apparently his calcium starvation treatment was not thoroughly effective in cutting off the supply of

calcium. Though the sand used was 99·5% insoluble in hydrochloric acid, yet the trees seem to have obtained a fairly adequate supply of calcium from the small amount present as impurity. Colby (7) states that trees, if partially starved of calcium, charge their tissues, especially their leaves, with silica, so that in sand-cultures silica may to some extent act as substitute for calcium. He found with trees of the French prune in water-cultures, that calcium starvation entirely prevented root growth.

Barker (2) found that apple trees did not grow well in an unaerated water-culture, large masses of callus developed on the roots which quickly became unhealthy and covered with bacterial slime. The trees subsequently died.

In preliminary experiments carried out at East Malling by the present author (17) with the object of finding a suitable way of growing apple trees in water-culture, three methods of aerating the culture solution were tried: (i) bubbles of air were passed continually through the solution from the centre of the bottom of the pot, (ii) the roots were suspended in the air and the solution was continuously and automatically sprayed over them, and (iii) the solution was continually circulated and aerated. The second method undoubtedly resulted in the most healthy root growth, but very good growth was also obtained with the first and third methods. The first method is much the simplest for extensive experiments and was therefore adopted for the present investigation.

In March 1938, maiden trees of Cox's Orange Pippin that had been budded on rootstocks Malling IX and Malling XII (dwarfing and vigorous, respectively) were cut back to a height of 2 ft. 6 in. The roots were carefully washed and the fibre removed. Individual trees were weighed and set up in jars of culture solution in an unheated glasshouse. The culture pots were four-gallon, glazed earthenware containers, and the covers were of wood painted with black asphaltum, the trees being held in place in them by loosely fitting split corks. Air was continuously supplied at the centre from the bottom of each pot, the air stream being broken up into a series of fine bubbles by means of a small alundum filter thimble.

There were eleven trees on each rootstock and each tree received 10 litres of solution, which was changed every two or three weeks, samples being taken for analysis at each change. Distilled water was added frequently to make good the losses due to transpiration and in order to keep the volume of solution constant. The composition of the culture solutions was: KNO_3, 0·005M; $Ca(NO_3)_2$, 0·005M; $MgSO_4$, 0·002M; KH_2PO_4, 0·001M, giving the following unit concentrations in p.p.m.: K=235, N=210, P=31, Ca=200 and Mg=49. Iron was added as ferric chloride and ferric citrate, 1 c.c. of a 0·5% solution of either being added per litre as required. In addition, traces of aluminium, iodine, bromide, titanium, tin, lithium, manganese, boron, zinc, copper, nickel and cobalt were added in a supplementary solution.

(2) Methods of Chemical Estimation.

Nitrogen. Nitrogen was estimated by the micro-Kjeldahl method as described by Pregl (18), nitrate being converted by the use of reduced iron.

Potassium. Potassium was estimated by the cobalt nitrate method as described by Hibbard and Stout (12), a check being made by the platinic chloride method.

RESULTS.

Growth of the Trees.

The trees were set up in March, at first in rain water, and within two weeks numerous new white roots were making their appearance. After this period the rain water was replaced by the full nutrient solution, and vigorous root growth

Table I.

Growth Records of maiden trees of Cox's Orange Pippin budded on Malling Rootstocks Nos. IX and XII grown in Water-Culture.

Record.	Rootstock.	Initial.	Final.	Increase.
Fresh weight (gm.)	IX XII	211 194	781 1,032	570 838
Scion diameter (cm.)	IX XII	1.28 1.16	1.78 2.07	0.50 0.91
Wood growth (cm.)	IX XII	— —	390 518	— —
Fruit buds (total per tree) ..	IX XII	— —	115 122	— —
Fruit buds (per metre growth)	IX XII	— —	20.2 14.6	— —

continued. The roots were remarkably free from fungus, shoot growth was normal and the leaves were healthy in appearance. Throughout the season weekly records were taken of fresh weight, and fortnightly records of diameters at 10, 35 and 50 cm. above the bud union. Leaf counts and lengths of leader shoots were recorded every three weeks.

Total Growth.

Table I shows the increase in fresh weight, wood growth and scion diameter during the season. The individual trees on each rootstock were originally of approximately the same weight. The mean initial fresh weight of those on No. IX rootstock was 211 gm., and that of those on No. XII was 194 gm. The characteristic effect of the rootstock in influencing the growth of the scion

was quite apparent in the water-cultures, increases in fresh weight, wood growth and stem diameter being much greater on the vigorous rootstock, No. XII.

In Fig. 1 the seasonal increases in fresh weight, basal diameter of the scion, and leaf area are plotted. It is evident from these curves that by far the largest

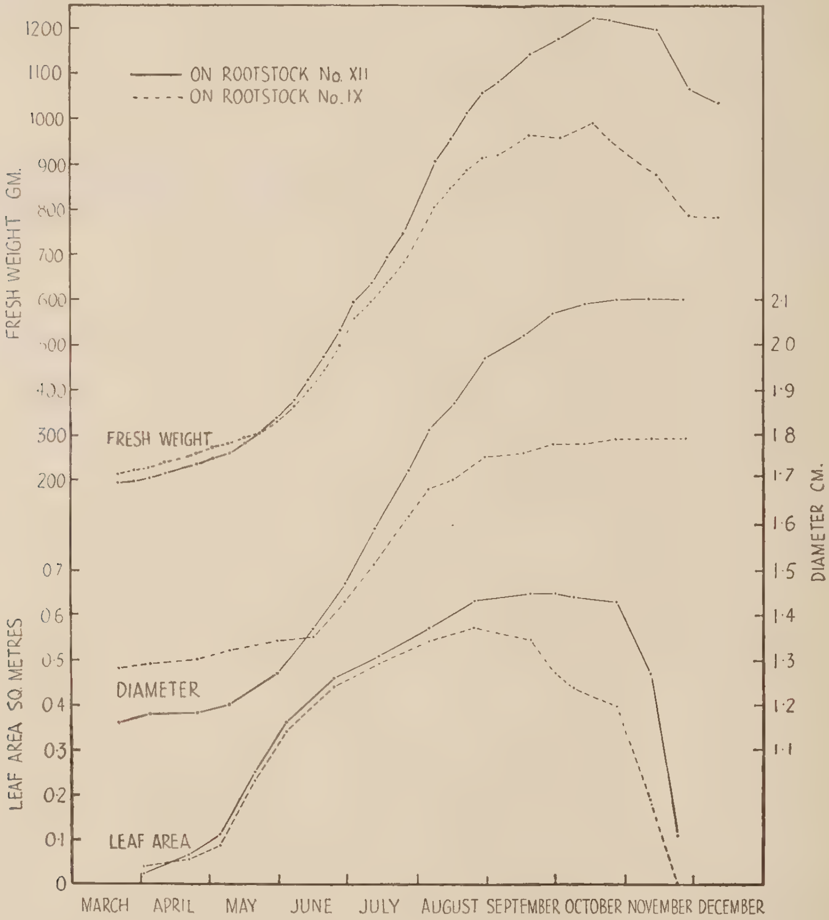


Fig. 1.

Seasonal changes of Fresh Weight of whole Tree, Diameter of Scion, and Leaf Area.

portion of the excess in increase in fresh weight and diameter of the trees on the vigorous rootstocks occurs during August and September. From the curve of leaf area it is clear that a decrease in total leaf area of the trees on No. IX begins soon after the establishment of the maximum, at the end of August; whereas the leaves on No. XII maintain a maximum area until the middle of

October. Some of the increase in growth of the trees on No. XII which occurs late in the season is therefore probably attributable to this maintenance of a large leaf surface and the consequent continued supply of carbohydrate.

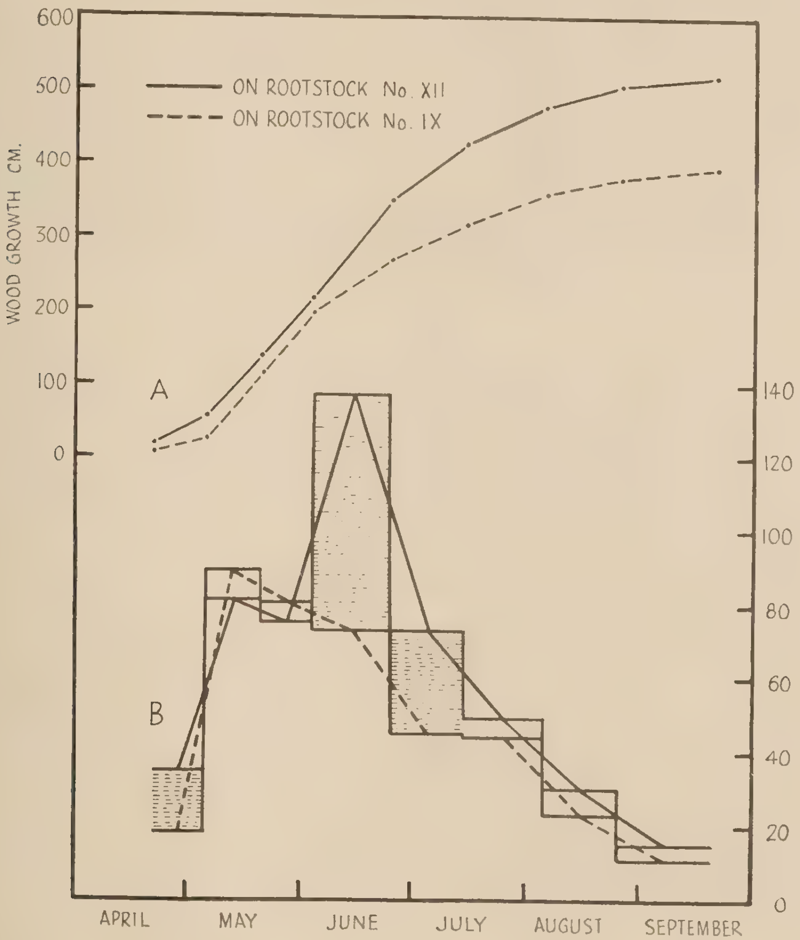


FIG. 2.

Seasonal Record of Wood Growth. A.—Total Wood Growth. B.—Periodical increments of wood growth. The periods when the shoots of the trees on No. XII rootstock are growing significantly faster than on No. IX rootstock is shown by the shaded areas.

WOOD GROWTH.

In Fig. 2 the seasonal values of wood growth are plotted, and also the amount of new growth made between each time of recording, which gives a measure of the rate of growth of the shoots. It is evident from this diagram that the only periods when the shoots of the trees on No. XII rootstock were

growing significantly faster than those on No. IX were at the end of April and the beginning of May, and also during the latter part of June and the beginning of July.

Increase in Diameter.

It was found that the top part of the scion near the point of origin of the young growing shoots begins to increase in girth earlier in the season than the more basal region. This fact is in accordance with the work of Knight (14) who showed that cambial activity is associated with proximity to the growing shoots. The relative increases in diameter at three positions on the scion given in Table II show (a) the very significant difference in the increase of the diameter of the trees on No. XII as compared with those on No. IX, and (b) that the

Table II.

Increase in Diameter.

Distance above union cm.	Average increase in diameter (1/10 mm.) Cox's/IX.	Cox's/XII.	Mean for position.	S.E. Diff. Position.
Top, 50 cm. ..	54·5	96.2	75·4	0.924
Middle, 35 cm. ..	53·6	93·4	73·5	Sig. Diff. 1.84
Base, 10 cm. ..	49·8	91·9	70·9	
Mean ..	52.67	93·88	S.E. Diff. Rootstock 3·683	

There are significant differences between top, middle and basal positions, both rootstocks behaving alike.

uppermost regions of the scion have increased during the season's growth more than the middle, and the middle more than the basal regions ; the trunk is thus becoming more cylindrical.

Fruit Buds.

The number of fruit buds produced was very large for two-year-old trees, and nearly all of them were axillaries. The trees on No. XII actually bore more fruit buds per tree than those on No. IX and the number of fruit buds per metre of wood growth was only slightly greater on the latter (Table I).

The growth records are not presented in detail in the present paper as nutritional considerations were the main object of this work. Sufficient data have been given, however, to show the usefulness of the hydroponic or water-culture method for growth studies with perennial plants.

VARIABILITY OF TREES IN WATER-CULTURE AND SIMILAR TREES IN SOIL.

In Table III a comparison is made between the growth of trees in water-culture and that of newly transplanted trees in soil. It is evident that the trees in salt solutions made much more growth than those in soil, probably largely because of (1) the longer growing period and higher temperatures prevailing in the glasshouse, and (2) the elimination of the retarding influence of drought which often adversely affects newly transplanted trees in the field. The variability of the trees in water-culture was rather less than that of those in soil.

WATER ABSORPTION.

The amount of water absorbed was measured throughout the season by means of a calibrated vertical tube fixed to each pot. The absorption rate per

TABLE III.

Comparison of Variability of Cox's Orange Pippin on Rootstocks IX and XII in the first year after Transplanting.

	Cox's/IX.			Cox's/XII.		
	No.	"V."	Growth cm.	No.	"V."	Growth cm.
Water-culture trees	11	14.6	390	11	16.9	518
Similar trees on Plot 17 ..	12	26.7	93	12	27.5	93
Plot 32	16	15.1	202	16*	20.6*	176*
Plot C.2, 2 year trees	128	27.7	244	64	22.5	400

* *Cox's on No. XVI.*

unit leaf area is plotted in Fig. 3, and was always greater for trees on No. XII than for those on No. IX. Knight (13) found no differences in the transpiration rates of detached leaves of the same age from the same variety on these same rootstocks, and the water content of such leaves was not usually significantly different. The difference in transpiration here, which is based on total leaf area, is therefore probably due to the differences in the proportions of leaves of various ages and of various positions which would naturally transpire at different rates.

The total water absorption for the season divided by the increase in fresh weight is shown in Table IV, and it is clear that the trees on No. XII absorbed less water per unit increase in fresh weight than those on No. IX. This is interesting since it has been suggested (29) that difficulty of passage of water through the No. IX union may to some extent explain the dwarfing effect of

this rootstock. Yet such trees absorb more water per unit increase of fresh weight than those on the vigorous rootstock No. XII.

Absorption of Nitrogen and Potassium.

The seasonal absorption of nitrogen and potassium is plotted in Fig. 4. It is evident that there is little difference in the actual course of absorption by the two rootstocks for either nitrogen or potassium, for the maximum is at the same period for each rootstock. In the early part of the season there is a

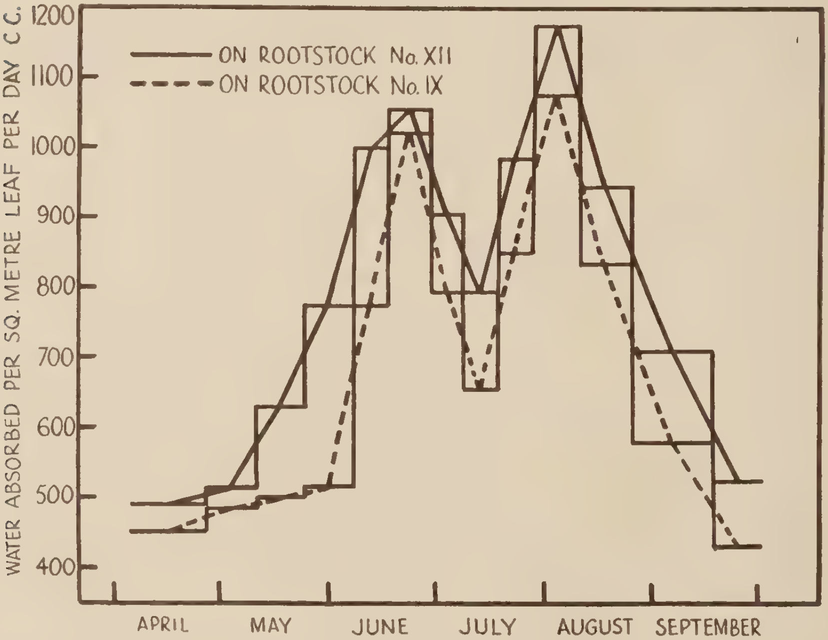


Fig. 3.
Seasonal Record of Water Absorption.

gradual increase in the absorption rate, irrespective of temperature, and at this stage internal factors seem mainly responsible for rate of absorption, the main factor probably being the then rapidly increasing absorbing surface as the roots grow. During the summer months the absorption rate shows a fair correlation with temperature, and this factor is then, presumably, of greater importance than the changing absorbing surface.

The curves for nitrogen and potassium absorption run fairly parallel ; but potassium absorption falls off fairly rapidly in the autumn whereas nitrogen absorption remains considerable until quite late.

THE RELATION BETWEEN FRESH WEIGHT AND THE ABSORPTION OF NITROGEN AND POTASSIUM.

In Fig. 5 the total amount of nitrogen and potassium that had been absorbed up to a known date is divided by the fresh weight at that date ; this

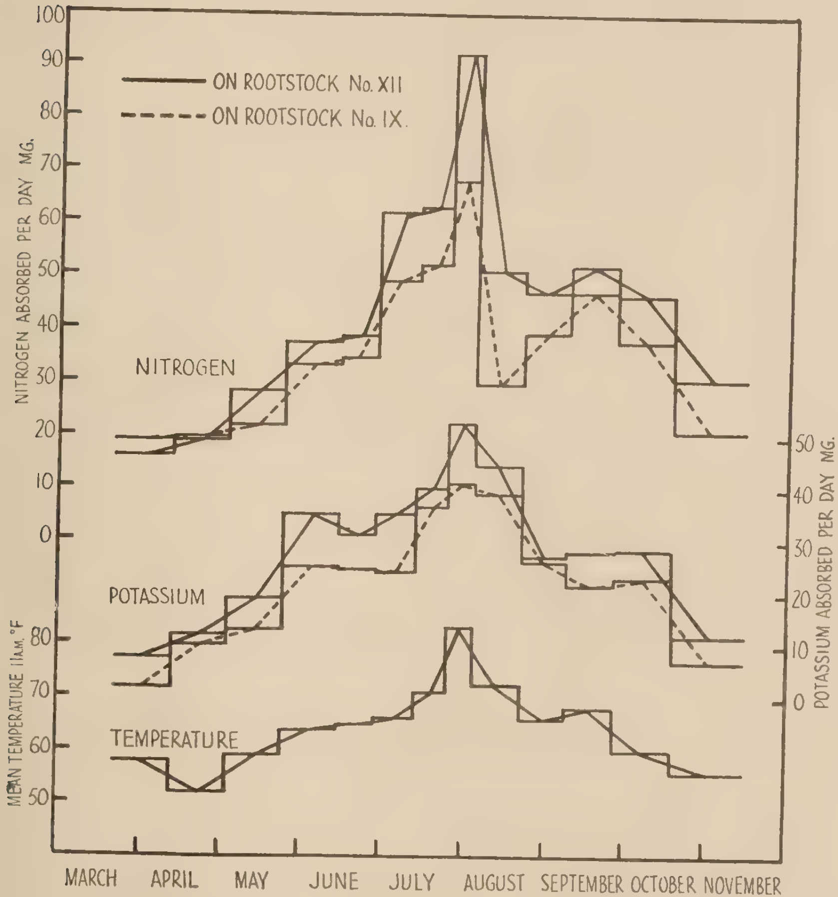


FIG. 4.
Seasonal Record of Absorption of Nitrogen and Potassium.

gives a measure of the amount absorbed per unit weight of tree. The diagram shows that while there is little difference at any period in the amount of nitrogen absorbed per unit of fresh weight for the trees on No. IX and those on No. XII, yet the trees on the vigorous rootstock, No. XII, absorbed considerably more

potassium early in the season. However, with the increasing growth of these trees, this difference disappeared towards the end of the growing season.

In consequence of this more rapid absorption of potassium the ratio of potassium absorption to nitrogen absorption is higher for trees on the vigorous rootstock until the end of August. This is in agreement with the work of Warne and Wallace (28) who collected samples of shoots from trees in July, and by chemical analysis of the material found that rootstocks promoting great vigour showed in July a high K/N ratio in the shoots.

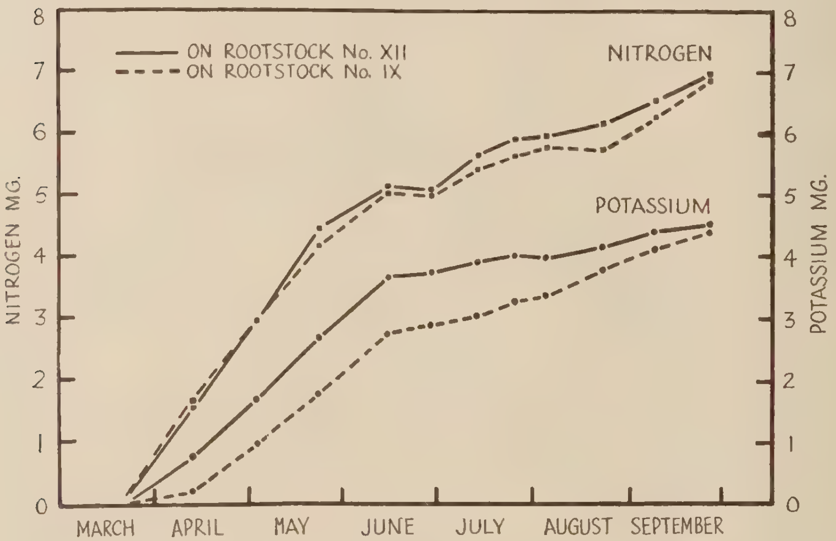


FIG. 5.
A Seasonal Record of the Relation between the Fresh Weight of Tree and the Total amount of Nitrogen and Potassium absorbed.

Quantitative Differences in Absorption.

It is clear from Table IV that the trees on No. XII rootstock absorb during the season nearly a third more of both nitrogen and potassium than those on No. IX. In this respect, then, the root system of the vigorous rootstock has supplied the scion with a greater quantity of nutrient than the dwarfing rootstock. However, the ratio of amount of growth made, either on the basis of fresh weight or of wood growth, shows that for both rootstocks the amount of growth made bears almost the same proportion to the amount of nutrient absorbed. The trees on No. IX absorbed rather more than those on No. XII for the amount of growth made, but the difference is not significant.

TABLE IV.

The Absorption of Water, Nitrogen and Potassium during the Growing Season (March to November) by Cox's Orange Pippin on Malling Rootstocks IX and XII in Water-Cultures.

	Cox's/IX.			Cox's/XII.		
	Total absorbed.	Absorption per unit fresh wt. increase.	Absorption per unit wood growth.	Total absorbed.	Absorption per unit fresh wt. increase.	Absorption per unit wood growth.
Water ..	56.018 litres.	100.18 c.c. pr. grm.	—	72.522 litres.	85.90 c.c. pr. gm.	—
Potassium ..	4.845 gm.	8.5 mg. per gm.	12.5 mg. per cm.	6.201 gm.	7.4 mg. per gm.	12.2 mg. per cm.
Nitrogen ..	8.037 gm.	14.1 mg. per gm.	20.7 mg. per cm.	9.972 gm.	11.9 mg. per gm.	19.2 mg. per cm.

DISCUSSION.

The water-culture method of growing plants for physiological studies, which has been widely used for exact experimentation with annual plants, has been relatively neglected for such studies with perennials. Apples would be expected to be especially difficult subjects for such culture as the roots are very sensitive to water-logging. In the present work, however, it has been shown that very good and uniform growth can be obtained provided the solution is continuously aerated. It is impossible to say definitely at present whether the beneficial effect of aeration is due merely to maintaining a high oxygen content in the solution, or to some indirect action such as the prevention of bacterial accumulation. If the cultures are not aerated, however, failure is certain, for the roots rapidly become covered with bacterial and fungal slime and die. The symptoms of ill-health are very similar to those exhibited by trees growing in waterlogged soil, which develop a malady known to growers as "the death".

With a suitable method of water-culture it has been shown that it is possible to grow healthy trees which are less variable than similar trees grown in the field. This is no doubt due to the more constant environment of the roots, and to the exclusion of such conditions as soil variation and root competition. This is a distinct advantage from the experimental standpoint, since a smaller number of trees is required to obtain significant differences, with the consequence that more extensive records can be taken without undue labour.

For nutritional experiments the water-culture method with trees has great possibilities, because with the rapid growth which takes place, especially under glasshouse conditions, deficiencies show up very quickly. In addition, at any

period during their life cycle, trees can be deprived of particular nutrients much more quickly and effectively than in either soil or sand-cultures.

The fact that in these experiments young trees of Cox's Orange Pippin on Malling rootstock No. XII flowered and fruited nearly as freely as similar trees on the dwarfing rootstock No. IX, although great differences in vigour still remained, raises a very interesting issue. It shows definitely that precocity is not of necessity linked with vigour. The factors responsible for this agreement between the two rootstocks are not of course clear from the present study, but the higher temperatures prevailing in the glasshouse may have played some part. It indicates, nevertheless, that water-cultures are a useful method of attack for studying the factors controlling fruit bud formation, and that the matter is worthy of further intensive investigation.

For quantitative studies in plant nutrition it is essential that the supply of nutrients to the trees should be accurately controlled, and water-culture is undoubtedly one of the best means of achieving this object.

The primary object of the present investigation was to determine if rootstock effect was at all explicable on the basis of the nutrients supplied to the scion by the root systems of the stocks. It has been shown that apart from an early accumulation of potassium by trees on the vigorous rootstock there is very little qualitative difference between the seasonal absorption cycles of nitrogen and potassium. On a quantitative basis, however, it is clear that the trees on No. XII rootstock absorb nearly one-third as much again of both nitrogen and potassium as those on No. IX. For both rootstocks the amounts absorbed bear almost exactly the same relation to the amount of growth made. It is therefore impossible at present to say whether more growth is made by the trees on the vigorous rootstock because its root system absorbs more nutrient, or whether more nutrient is absorbed because more growth is made. Further light could perhaps be thrown on this issue by altering the concentrations of the solutions supplied. Absorption is to some extent controlled by the concentration, so that with suitable solutions it should be possible to restrict the nutrient supply to the trees on the vigorous rootstock and augment the supply to those on the dwarfing rootstock ; their differential behaviour at several levels of nutrient supply could thus be studied.

SUMMARY.

1. A method of growing apple trees in water-culture is described and the advantages of this procedure for growth and nutritional studies is indicated.

2. Maiden trees of Cox's Orange Pippin budded on Malling rootstocks No. IX (dwarfing) and No. XII (vigorous) were successfully grown in continuously aerated aqueous solutions.

3. The variability in development of the trees was less than that of similar trees in soil.

4. The usual effect of the rootstock type in controlling the degree of vigour of the tree was not affected by the method of culture.

5. Trees on the vigorous rootstock, No. XII, bore blossom as freely as those on the dwarfing rootstock, No. IX.

6. Trees on No. XII rootstock absorbed more water per unit leaf area throughout the growing season than those on No. IX.

7. Trees on No. IX rootstock absorbed more water per unit increase in fresh weight than trees on No. XII.

8. There was little qualitative difference in the course of nitrogen and potassium absorption for the two different types of tree.

9. Trees on No. XII absorbed considerably more potassium per unit weight of tree in the early part of the growing season.

10. While the trees on the vigorous rootstock absorbed considerably more potassium and nitrogen, the ratio of total growth made to the amount of each of these nutrients absorbed did not differ significantly for the trees on the two rootstocks.

LITERATURE REFERENCES.

(1) *Bain, S. M.* The action of copper on leaves. Bull. Tenn. Agric. Expt. Sta., 1902, **15**, 21.

(2) *Barker, B. T. P.* Studies on root development. Long Ashton Res. Sta. Ann. Rep. for 1921, 9.

(3) *Bauer, H.* Stoffbildung und Stoffaufnahme in jungen Nadelhölzern. Naturw. Z. Forst- u. Landw., 1910, **8**, 457.

(4) ———. Stoffbildung und Stoffaufnahme in jungen Laubhölzern. Naturw. Z. Forst- u. Landw., 1911, **9**, 409.

(5) ———. Zur Periodizität der Stoffbildung und Nährstoffaufnahme in jungen Laubhölzern. Naturw. Z. Forst- u. Landw. 1912, **10**, 188.

(6) *Chandler, R. F. (Jr.)* Absorption, distribution and seasonal movement of potassium in young apple trees and the effect of potassium fertilizer on potassium and nitrogen content and growth of trees. Journ. Agric. Res., 1936, **53**, 19.

(7) *Colby, H. L.* Seasonal absorption of nutrient salts by the French prune grown in solution culture. Plant Physiol., 1933, **8**, 1.

(8) *Combes, R.* Absorption et migrations de l'azote chez les plantes ligneuses. Ann. Physiol. Physicochim. biol., 1927, **3**, 333.

(9) *Duhamel du Monceau, H. L.* La physique des arbres., 1758, **2**, 202.

(10) *Hatton, R. G.* and *Grubb, N. H.* Field observations on the incidence of Leaf Scorch upon the apple. Journ. Pom. & Hort. Sci., 1924-5, **4**, 65.

(11) *Hatton, R. G.* Apple rootstock studies. Journ. Pom. & Hort. Sci., 1935, **13**, 293.

(12) *Hibbard, P. L.* and *Stout, P. R.* Estimation of potassium by titration of the cobaltinitrite with potassium permanganate. Journ. Ass. Off. Agric. Chem., Wash., 1933, **16**, 137.

(13) *Knight, R. C.* Water relations of stocks and scions. East Malling Res. Sta. Ann. Rep. for 1924 (1925), 103.

(14) ———. The relation in the apple between the development of young shoots and the thickening of older stems. Journ. Pom. & Hort. Sci., 1927, **6**, 72.

(15) *Mann, C. E. T.* The physiology of the nutrition of fruit trees. I. Some effects of calcium and potassium starvation. Long Ashton Res. Sta. Ann. Rept. for 1924, 30.

(16) *Nobbe, F.* Ueber den Wasserverbrauch zweijahriger Erlen unter verschieden Beleuchtungs-Bedingungen. Landw. Vers. Sta., 1881, **26**, 354.

(17) *Pearse, H. L.* Apple trees in water culture. East Malling Res. Sta. Ann. Rept. for 1936 (1937), 131.

(18) *Pregl F.* Quantitative organic microanalysis. J. & A. Churchill, London, 1924.

(19) *Reed, H. S.* and *Haas, A. R. C.* Nutrient and toxic effects of certain ions on citrus and walnut trees. Tech. Pap., Calif. Agric. Expt. Sta., 1924, 17.

(20) *Roberts, R. H.* Experiments upon apple tree nutrition. Proc. Amer. Soc. Hort. Sci., 1920, **17**, 197.

(21) ———. Nitrogen reserve in apple trees. Proc. Amer. Soc. Hort. Sci., 1921, **18**, 143.

(22) *Thomas, W.* Nitrogenous metabolism of Pyrus malus L. IV. The effect of sodium nitrate applications on the total nitrogen and its partition products in the leaves, new and one year branch growth throughout a year's cycle. Plant Physiol., 1927, **2**, 245.

(23) *Vaidya, V. G.* The seasonal cycles of ash, carbohydrate and nitrogenous constituents in the terminal shoots of apple trees and the effects of five vegetatively propagated rootstocks on them. I. Total ash and ash constituents. Journ. Pom. & Hort. Sci., 1938, **16**, 101.

(24) *Wallace, T.* Experiments on the manuring of fruit trees. Journ. Pom. & Hort. Sci., 1924, **4**, 117; and 1925, **5**, 1.

(25) ———. Investigations on chlorosis. Journ. Pom. & Hort. Sci., 1928, **1**, 162; and 1929, **1**, 251.

(26) ———. Leaf Scorch on fruit trees. Journ. Pom. & Hort. Sci., 1927-8, **6**, 243; and 1928-9, **7**, 1.

(27) ———. The effects of deficiencies of potassium, calcium and magnesium respectively, on the contents of these elements and phosphorus in the shoot and trunk regions of apple trees. Journ. Pom. & Hort. Sci., 1930, **8**, 23.

(28) *Warne, L. G. G.* and *Wallace, T.* The composition of the terminal shoots and fruits of two varieties of apple in relation to rootstock effects. Journ. Pom. & Hort. Sci., 1935, **13**, 1.

(29) *Warne, L. G. G.* and *Raby, J.* The water conductivity of the graft union in apple trees, with special reference to Malling rootstock No. IX. Journ. Pom. & Hort. Sci., 1939, **16**, 389.

(30) *Wolff, E.* and *Knop, W. W.* Zweiter Ber. d. landw. Inst. Leipzig. (Sachs. Agr. Chem. 449, Leipzig, 1888.)

(*Received* 2/10/39.)

THE INCORPORATION OF GROWTH HORMONES IN SEED DRESSINGS

By H. E. CROXALL and L. OGILVIE
Research Station, Long Ashton, Bristol

RECENT researches have indicated that the application of growth hormones to seeds may stimulate the growth of the resulting plants (1, 2, 4, 10, 11) and may result in higher crop yields (3). It has also been claimed (6) that the injurious effect of steeping cereal seed in copper sulphate solution or in formalin may be overcome by including small quantities (up to 5 p.p.m.) of growth hormones in the solutions.

The authors had already acquired considerable knowledge of the effects of the application of cuprous oxide and mercurial dressings in powder form to the seeds of various vegetables, particularly peas; and the main object of the present investigation was to determine whether growth hormones can be incorporated with advantage in these dressings. This paper therefore presents studies on the effect of a number of different combined dressings on the germination and subsequent development of several varieties of peas and one of dwarf beans.

MATERIALS AND METHODS.

It was realized at the outset that the application to seeds of phytohormones in solution would not be feasible on a commercial scale, and all the preparations used were therefore in the form of dry powders (dusts). These can be applied more easily to seeds, and the dressed seeds can be stored until sowing conditions are favourable.

The growth-promoting substances employed were α-naphthalene-acetic acid, mixed naphthylidene-acetic acids, and β-indolyl-butyric acid. They were incorporated in various concentrations with the following: talc, a proprietary mercurial seed dressing, cuprous oxide and zinc oxide. A list of the mixtures is given in Table I.

The mercurial and zinc oxide dressings containing phytohormones were supplied by the manufacturers of the mercurial dressing. The cuprous oxide and talc dressings were prepared as follows: Solutions of the pure hormones were made in acetone and were diluted to the required concentrations. The volume of acetone used was such that a thin paste could be made with the requisite weight of talc or finely divided cuprous oxide. The hormone solution was then mixed thoroughly with the paste, the acetone allowed to evaporate

and the dressings re-powdered and shaken. To ensure that no acetone remained, the dusts were allowed to remain exposed to the air for a fortnight before use.

Tests were made to determine whether acetone itself had any effect on the seed dressings. Cuprous oxide and talc were treated with pure acetone alone in the manner described above. The dressings were then applied to pea seeds, and the rate of germination in Petri dishes and the percentage emergence of the seedlings in soil were compared with those of seed dusted with untreated cuprous oxide and talc respectively. No differences in the percentages or in the rates

TABLE I.

Composition of Seed Dressings used in the Experiments.

Number.	Hormone.	Conc. of hormone (p.p.m. of base).
A. Mixtures with talc as a base.		
T1	α-naphthalene-acetic acid.	5
T2	,, ,,	10
T3	mixed naphthylidene-acetic acids.	5
T4	,, ,,	10
T5	β-indolyl-butyric acid.	5
T6	,, ,,	10
T7	α-naphthalene-acetic acid.	20
T8	mixed naphthylidene-acetic acids.	20
T9	α-naphthalene-acetic acid and mixed naphthylidene-acetic acids.	10 of each.
T10	α-naphthalene-acetic acid, mixed naphthylidene-acetic acids, and β-indolyl-butyric acid.	6·6 of each.
T11	α-naphthalene-acetic acid and mixed naphthylidene-acetic acids.	5 of each.
B. Mixtures with a mercurial dressing as a base.		
M1 to M11	Composition as in T1-T11 but with a proprietary mercurial dressing instead of talc.	
C. Mixtures containing cuprous oxide as a base.		
C1 to C11	Mixtures with the same hormone content as T1-T11 in the talc series.	
D. Mixtures containing zinc oxide as a base.		Conc. of hormone (p.p.m. of base).
Z7	α-naphthalene-acetic acid.	20
Z8	mixed naphthylidene-acetic acids.	20
Z9	α-naphthalene-acetic acid and mixed naphthylidene-acetic acids.	10 of each.
Z11	,, ,, ,, ,, ,, ,,	5 of each.

of germination were observed, indicating that the acetone alone had no effect on the seed dressings.

All the seeds were treated by the following method: The seeds and dust were placed in glass stoppered bottles and shaken on a rotary shaker for 500 revolutions at 36 revolutions per minute. The amount of dust used was 0·5% by weight of the seed. This amount was in excess, since when even larger quantities were used the weight of it adhering varied from 0·25%-0·4% of the weight of the seed, depending on the variety used, but was usually about

0·3%. This means that when a dressing containing 10 p.p.m. of hormone was used, 3 parts of hormone were applied to 100 million parts by wt. of seed.

Germination tests of treated and untreated seeds were carried out at laboratory temperature on moist filter paper in Petri dishes. Fifty seeds were placed in each dish, and in each experiment the same volume of water was added to each dish. The seeds were removed from the dishes when the radicle was 1·0 cm. long.

Sowings in the greenhouse were made in boxes of soil, measuring $14 \times 9 \times 2$ in. In sowing, the top 1 in. of soil was removed, the seeds then placed on the exposed surface and the boxes refilled to the top. In this way all the seeds were sown as nearly as possible at a uniform depth. Unless otherwise stated, fifty seeds were sown in each box.

In field trials the seeds were sown by hand about 1 in. apart in drills 1-2 in. deep and 3 feet apart.

Previous experiments had shown that different varieties of peas reacted in different ways to mercurial and cuprous oxide dressings. Certain early, round-seeded varieties were more resistant to pre-emergence damping off, and did not benefit so much from the application of seed dressings as did some wrinkled-seeded varieties. The difference in the effect of the dressings on different varieties under various conditions was so great that in order to test as thoroughly as possible the effect of the hormone-containing dusts the commonly grown varieties of peas mentioned below were used.

LABORATORY GERMINATION TESTS.

The following varieties of peas were used:—

Round-seeded. British Lion, Early Bird, Eclipse, Foremost.

Wrinkled-seeded. Admiral Beatty, Progress, The Lincoln.

Batches of fifty untreated seeds and of fifty treated with the mercurial dressing and with each of the hormone-containing dressings M1, M2, M3, M9, M5 and M6 were allowed to germinate in Petri dishes.

There was no consistent difference in any variety between the rate of germination of the controls and that of the treated seeds, and the number of seeds germinating was almost exactly the same in any treatment as in the controls, whilst there was no apparent injurious effect with any of the mercurial dressings.

When seeds of these six varieties were treated with cuprous oxide some of them failed to germinate in Petri dishes. The percentage germination of treated and untreated seeds in two trials is given in Table II.

It will be seen that there is considerable difference in the susceptibility of different varieties to damage by cuprous oxide. The variety Eclipse was the most susceptible and it was used for further investigation.

TABLE II.

Germination (%) in Petri Dishes of Pea Seeds treated with Cuprous Oxide.

Variety.	Seeds on wet filter paper.		Seeds completely immersed in water.	
	Control.	Cuprous oxide.	Control.	Cuprous oxide.
Admiral Beatty ..	100	84	94	68
British Lion	96	92	98	66
Early Bird	96	90	90	76
Eclipse	96	58	98	24
Foremost	98	86	98	72
Progress	84	82	94	66
The Lincoln	96	86	90	74

The injurious effect of cuprous oxide appeared to be due to the entry of copper through the micropyle and not through the seed coat. This was indicated by the following experiment. Two hundred seeds of Eclipse were treated with cuprous oxide. One hundred were placed in Petri dishes with the micropylar side of the seed in contact with wet filter paper. The second hundred were placed on wet filter paper with the micropylar side uppermost, the upper surface being left dry. One hundred untreated seeds were placed under similar conditions. Table III gives the percentage germination in each case.

TABLE III.

Germination in Petri Dishes of Pea Seeds treated with Cuprous Oxide.

Untreated Seeds.	Treated Seeds.	
Control.	Micropyle on wet filter paper.	Micropyle dry.
98	2	96

The number of seeds failing to germinate was high when they were completely immersed (Table II), as in this case all the micropyles were in contact with water.

In order to determine the effect of cuprous oxide dressings containing hormones, lots of seeds of the variety Eclipse were dressed with cuprous oxide alone, and with each of the dressings C1-C6 containing hormones. The treated seeds and untreated control were immersed in water for twelve hours, and the excess water then removed. The percentages of germination are given in Table IV.

Under these experimental conditions no reduction in the injurious effect of the cuprous oxide was obtained by incorporating hormones with the dressings, and there was no indication that such incorporation stimulated germination.

TABLE IV.

Germination (%) in Petri Dishes of Pea Seeds treated with Cuprous Oxide without and with Hormones.

Control.	Cuprous oxide.	C1.	C2.	C3.	C4.	C5.	C6.
98	26	22	18	16	12	16	10

GREENHOUSE EXPERIMENTS.

Further experiments were conducted to determine whether the rate of growth of seedlings after germination was influenced by the application to the seed of dressings containing hormones. Seeds of the varieties Admiral Beatty, British Lion, Eclipse, Foremost and The Lincoln, were treated with the mercurial dressing and with each of the hormone-containing dressings M1-M6. The treated and untreated seeds were sown in boxes of sterile soil. This was necessary for two reasons. In ordinary soil the number of control seedlings that failed to emerge was so large as to make comparison between treatments and controls difficult. There was also the possibility that, since, in ordinary soil, the cotyledons of seeds treated with a mercurial dressing alone are preserved for a longer period than those of controls, the seedlings from treated seeds would make more rapid growth owing to the greater food reserve available. The use of sterile soil avoids these difficulties.

The number of seedlings that emerged each day was counted. From the figures obtained coefficients of the rate of emergence for each of the treatments for each variety were calculated by means of the formula devised by Kotowski (7). These differed for each variety, e.g. that for Eclipse was higher than that for The Lincoln, when grown under identical conditions. Moreover, the coefficients for any one variety vary with different external conditions, such as changes of temperature. In order to obtain as close a comparison as possible of the effects of the different dressings the coefficient of rate of emergence from the untreated seed of each variety was therefore fixed at 100 and the coefficients for each of the treatments equated.

The coefficients calculated in this way for each of the varieties used are given in Table V.

It will be seen that the different varieties respond in different degrees to these treatments, Admiral Beatty being much more stimulated by the hormone treatment than any other variety. Moreover, the treatment which gave the maximum response with one variety did not necessarily give the greatest stimulation with the others.

The mercurial dressing alone appeared to accelerate slightly the rate of emergence from the four varieties Admiral Beatty, British Lion, Early Bird

TABLE V.

Coefficients of Rate of Emergence from Treated and Untreated Pea Seeds.

Treatment.	Admiral Beatty.	British Lion.	Early Bird.	Eclipse.	Fore-most.	The Lincoln.	Average.
Control ..	100	100	100	100	100	100	100
Mercurial dressing	106	104	104	104	100	96	102
M1 ..	112	106	113	99	112	108	109
M2 ..	123	114	108	111	103	105	111
M3 ..	124	105	107	102	112	101	101
M4 ..	129	104	108	109	113	112	113
M5 ..	125	105	98	98	105	105	106
M6 ..	106	90	100	96	112	98	100

and Eclipse. There was no acceleration in the rate of emergence from the variety Foremost, while with The Lincoln there appeared to be a slight check.

The dressing M1, containing 5 parts per million of α-naphthalene-acetic acid, gave a higher coefficient than the mercurial dressing alone with each of the varieties used. M2, which contained 10 parts per million of the same acid, caused consistently greater stimulation than the mercurial dressing. With three varieties a higher coefficient was given than with M1, and with the other three a somewhat lower one. It seems that, so far as rate of emergence is concerned, for the varieties Foremost, The Lincoln and Early Bird, 10 parts per million of α-naphthalene-acetic may exceed the optimum concentration.

The dressing M3, containing 5 parts per million of naphthylidene-acetic acids, gave similar results to M1, although there were differences in that some varieties showed slightly less and some slightly more stimulation with it.

M4, containing 10 parts per million of mixed naphthylidene-acetic acids, caused about the same stimulation as M3 or a greater one.

Treatment with dressing M5, containing 5 parts per million of β-indolyl-butyric acid, was not so beneficial as that with the hormone-containing dressings M1, M2, M3 and M4. In only three cases were better results obtained than with the mercurial dressing alone.

M6, containing 10 parts per million β-indolyl-butyric acid, gave even poorer results than M5, except with the seeds of one variety ; and it appears that 10 parts per million exceeds the optimum concentration of this substance under the conditions of the experiment.

After three weeks the seedlings were removed from the boxes and the soil was washed from the roots, care being taken to damage them as little as possible. The seedlings were dried at 100° C. and weighed, and the average dry weight of each calculated. The average dry weight of the controls of each variety

was taken as 100. In Table VI are given the average dry weights for each treatment on six varieties, calculated as a percentage of the dry weight of the control seedlings.

Here again, the different varieties were not affected to the same degree by the dressings, Admiral Beatty being stimulated considerably more than any other. It can also be seen that no single dressing produced the optimum effect on all the varieties, although several dressings gave consistently good results on each variety. The mercurial dressing alone stimulated the growth of the seedlings of each variety, but the dressings containing α-naphthalene-acetic acid and that containing mixed naphthylidene-acetic acids had an even greater effect. The seedlings from seed treated with dressings M1 and M3 were, except in the variety British Lion, heavier than those from seed treated with the mercurial

TABLE VI.

Average Dry Weight of Seedlings from Treated Seeds after Three Weeks.

Treatment.	Admiral Beatty.	British Lion.	Early Bird.	Eclipse.	Fore-most.	The Lincoln.	Average of 6 vars.
Control ..	100	100	100	100	100	100	100
Mercurial dressing	138	128	128	120	106	102	120
M1 ..	149	126	132	126	112	119	127
M2 ..	168	148	118	156	127	127	141
M3 ..	174	126	138	129	109·5	111	131
M4 ..	177	135	142	159	131	151	149
M5 ..	157	121	112	109	118	125	124
M6 ..	123	72·5	98	104	144	120	110

dressing alone. The dressings M2 and M4, containing higher concentrations of these hormones, usually gave a greater increase in weight. The average percentage dry weight with treatment M2 was 21%, and with M4, 29%, greater than the percentage weight of plants produced from seeds with a mercurial dressing alone.

On one variety, Early Bird, the dressing M2, containing 10 parts per million of α-naphthalene-acetic acid, was less effective than M1, containing 5 parts per million of it. This again indicates that, at least with some varieties, 10 parts per million exceeds the optimum concentration. The dressings M5 and M6 containing β-indolyl-butyric acid gave very varying results. With three varieties only did M5 give heavier seedlings than the mercurial treatment. M6 caused greater stimulation than M5 on only one of these varieties, viz. Foremost ; and with all the varieties except this one the seedlings were not as heavy as those from seed treated with the mercurial dressing alone. The development of seedlings of British Lion was retarded considerably in comparison with that of the control seedlings of this variety. It appears that indolyl-butyric acid, in

concentrations of 5-10 parts per million, may be applied with safety to seeds of only a limited number of pea varieties.

Further sowings in boxes of sterile soil were made, using the varieties Foremost (round-seeded) and Surprise (wrinkled-seeded). The seeds of each variety were treated with each of the following dressings: talc, cuprous oxide, the mercurial dressing and each of the hormone-containing dressings, T1-T6, C1-C6 and M1-M6. The coefficients of rate of emergence were calculated as before and are given in Tables VII and VIII, where rates are expressed as percentages of the control coefficient.

TABLE VII.

Coefficients of Rate of Emergence from Treated and Untreated Seeds, var. Foremost.

Treatment.	Coefficient.	Treatment.	Coefficient.	Treatment.	Coefficient.
Talc	100	Cuprous oxide	92·5	Mercurial dressing	92
T1	119	C1	109	M1	93
T2	117·5	C2	108	M2	98
T3	102·5	C3	92	M3	109
T4	114	C4	119	M4	99
T5	102	C5	92	M5	107
T6	109	C6	102	M6	107

It can be seen that the dressings T1, T2 and T4 considerably accelerated the rate of emergence. The effect of the cuprous oxide and mercurial dressings without hormones was to retard emergence. This apparently disagrees with the

TABLE VIII.

Coefficients of Rate of Emergence from Treated and Untreated Seeds, var. Surprise.

Treatment.	Coefficient.	Treatment.	Coefficient.	Treatment.	Coefficient.
Talc	102	Cuprous oxide	94	Mercurial dressing	95
T1	97	C1	103	M1	100
T2	98	C2	95	M2	106
T3	106	C3	97	M3	100
T4	95	C4	98	M4	111
T5	98	C5	94	M5	101
T6	103	C6	95	M6	97

results of the previous experiment, but this one was conducted under conditions of high temperature, and a number of tests under these conditions indicated that the mercurial dressing lowered the rate of emergence. The effect of incorporating hormones with both the cuprous oxide and the mercurial dressings was

to raise the coefficients of rate of emergence to that of the control and above it. With cuprous oxide treatments, except the mixture C4, all the coefficients were from 7 to 10% lower than those of the corresponding treatments in the talc series. C4 gave an even better result than the talc mixture T4.

The results with the mercurial dressings containing hormones were similar to those previously obtained with the same dressings on this variety, except that M4, with 10 parts per million of naphthylidene-acetic acids, was less effective than M3, containing 5 parts per million.

The results with the variety Surprise were rather different from those with Foremost. The mixtures T1 and T2 tended to depress slightly the rate of emergence, and this effect was even more noticeable with the mixture T4. This appears to indicate that these concentrations of the hormones at high temperatures may check growth, especially in the early stages.

Treatment with mercurial and with cuprous oxide dressings alone, again retarded the emergence of the seedlings.

The dressings containing hormones produced an acceleration in growth in some cases. In the cuprous oxide series C1 was most effective; C2 and C3 slightly accelerated the rate of emergence, while C2, C5 and C6 had no effect.

Of the mercurial dressings, M4 caused considerable stimulation, while M1, M2 and M5 all gave a coefficient of emergence equal to or greater than the controls. M6, containing the higher concentration of β-indolyl-butyric acid, caused no perceptible stimulation.

The plants of both varieties were kept until they flowered and formed pods. There was no appreciable difference in the time of flowering under any of the treatments, indicating that stimulation may be confined to vegetative growth. After fifty-four days the pods were collected and weighed. Their weights, expressed as per cent. of weight of pods from control plants, are given in Tables IX and X.

The effect of the limited quantity of soil in which the plants were growing detracts somewhat from the value of these results, and similar ones would not

Table IX.

% Weight of Pods after 54 days, var. Foremost.

Treatment.		Treatment.		Treatment.	
Talc	100·5	Mercurial dressing	92·4	Cuprous oxide	96·7
T1	130·1	M1	109·6	C1	124·7
T2	116·1	M2	102·7	C2	99·4
T3	120·4	M3	118·2	C3	106·4
T4	107·5	M4	97·8	C4	105·3
T5	106·4	M5	102·5	C5	104·8
T6	108·2	M6	95·7	C6	103·6

TABLE X.

% Weight of Pods after 54 days, var. Surprise.

Treatment.		Treatment.		Treatment.	
Talc	98·8	Mercurial dressing	72·2	Cuprous oxide	95·5
T1	112·2	M1	93·3	C1	113·3
T2	104·4	M2	97·7	C2	101·1
T3	141·1	M3	81·1	C3	94·4
T4	90·0	M4	90·0	C4	98·8
T5	97·7	M5	94·4	C5	103·3
T6	93·3	M6	88·8	C6	102·2

necessarily have been obtained in the field. They do, however, indicate that the stimulation caused by the hormone-containing dressings was not limited to the early stages of growth only, and that greater crop weights may be obtained by the use of these dressings.

With the variety Foremost the greatest weights of pods were obtained from the seeds treated with dressings containing 5 parts per million of α-naphthalene-acetic acid and 5 parts per million of mixed naphthylidene-acetic acids. This indicates that although the mixture containing 10 parts per million of these substances may produce more rapid emergence than those containing weaker concentrations (see Table VII, treatments M2, T4, C4), a more persistent effect may be obtained by using only 5 parts per million of the hormones in the dressing.

The results obtained with the variety Surprise were slightly different. Of the talc dressings, T1 and T3 again gave the best results, but here T1 was less successful than T3, while the reverse was the case with the variety Foremost. The weaker concentrations of α-naphthalene-acetic and mixed naphthylidene-acetic acids, however, were still the most effective.

Of the mercurial and cuprous oxide series of dressings, M2, M4 and C4 gave a somewhat greater weight of pods than the dressings M1, M3 and C3, respectively, which contained smaller quantities of the two hormones. Moreover, the dressings C5 and C6, containing indolyl-butyric acid, appeared to be more effective than the corresponding dressings T5 and T6 of the talc series. A possible explanation of this may be that the persistent check produced by the mercurial and cuprous oxide dressings alone on this variety under these experimental conditions may be overcome only by the use of higher concentrations of hormones.

Another trial was conducted with the variety Eclipse, the development of which was known to be checked by applications of cuprous oxide to the seed. It was discovered that when the soil moisture was below 20% saturation capacity, 20 to 30% of the treated seeds failed to germinate. When the soil moisture

content was greater than 20% of saturation the percentage germination was the same as that of untreated seed, but the rate of emergence was slower.

Petri dish experiments showed that actual killing of the seed was not prevented by incorporating the hormones in the dressing, and under normal sowing conditions in the field the soil is usually sufficiently moist so that there is little danger of failure to germinate. Hence the following experiment was devised to ascertain whether the check to the rate of emergence could be overcome by using cuprous oxide dressings containing hormones. Seeds were treated with cuprous oxide and each of the hormone-containing dressings C1, C2, C3, C4, C5 and C6. They were sown in boxes of sterile soil which was maintained at about 50% of its saturation capacity. Coefficients of rate of emergence were calculated as before, and together with final percentage emergences are given in Table XI.

TABLE XI.

% Emergence from Seeds treated with Cuprous Oxide and Hormones.

Treatment.		Coefficient of rate of emergence.
Control	91	100
Cuprous oxide	93	86
C1	93	98
C2	90	94
C3	91	90
C4	96	97
C5	92	94
C6	92	90

It can be seen from these results that the hormone-containing dressings, especially C1 and C4, gave considerably higher coefficients than cuprous oxide alone, and that the coefficients of the former closely approach those of the control.

Experiments were made to determine the effect of the hormone-containing dressings on the emergence from seeds sown under conditions favourable to pre-emergence damping-off. The seeds were sown in well mixed greenhouse soil known to be highly contaminated with fungi, especially species of Pythium which cause damping-off. Seeds of Early Bird (round-seeded) and The Lincoln (wrinkled-seeded) were treated with the proprietary mercurial dressing and with the mercurial dressings containing hormones M1-M6. The treated and the untreated (control) seeds were sown 1 in. deep and the boxes were watcred heavily immediately after sowing. The temperature of the greenhouse was between 68° F. and 76° F. during the experiment. The final percentage emergences for the different treatments are given in Table XII.

TABLE XII.

% Emergence from Seeds sown in Non-Sterile Soil.

Treatment.	Early Bird.	The Lincoln.
Control	66	24
Mercurial dressing	82	52
M1	86	76
M2	90	82
M3	90	62
M4	76	70
M5	88	70
M6	80	74

With the variety Early Bird, the dressings M2 and M3 gave only slight increases in the final percentage emergence. The seedlings from seeds treated with these two dressings and also from those treated with M1 and M4 were more vigorous than those from untreated seeds and from seeds treated with mercurial dressing alone.

More striking results were obtained with the variety The Lincoln. Treatment with the dressings containing hormones, especially M1, M2, M4, M5 and M6, caused a much higher percentage of emergence than did treatment with the mercurial dressing alone. The seedlings also continued to grow more vigorously. The difference in the reaction of these two varieties to the hormone-containing dressings is probably due to the fact that Early Bird germinates very rapidly and is therefore only slightly susceptible to pre-emergence damping-off, while The Lincoln is very slow in germinating and therefore very susceptible to it.

The variety The Lincoln was used in further experiments in order to determine the effect of including higher concentrations of α-naphthalene-acetic and mixed naphthylidene-acetic acids in the dressings, and also the effect of mixtures of hormones in a single dressing. Zinc oxide alone and containing hormones was also used, in order to determine whether this substance could satisfactorily be substituted for the poisonous mercurial dressings.

Seeds were treated with each of the following dressings: mercurial dressing and the mercurial dressings containing hormones M1-M9 and M11; cuprous oxide and the hormone-containing dressings C1-C10 inclusive; talc and the corresponding hormone dressings T1-T10; zinc oxide and the hormone-containing dressings Z7, Z8, Z9 and Z11. The seed was sown in soil similar to that used in the previous experiment. The soil was heavily watered each day, i.e. kept almost saturated throughout. The temperature fluctuated between 70° and 84° F., and was somewhat higher than in the previous experiment.

The talc series of treatments gave no reliable information on the comparative efficiency of the different hormone treatments since not more than

12% of the seeds emerged with any treatment. Most of the seed rotted before germination took place. This result is in agreement with those of the previous experiments which indicated that the hormones did not accelerate germination, but stimulated growth after the seed had germinated. As only a small proportion of the seeds germinated, no great increase of stand could be expected as a result of the application of hormones without any protective fungicide.

The zinc oxide treatments also failed to yield any favourable result. Only 26% of the seedlings emerged from the treated seeds, and no greater emergence was obtained from seeds treated with the zinc oxide dressings containing hormones. This result may have been due to the slight protective effect of the zinc oxide and also to the concentration of hormones, 20 parts per million, having perhaps been too high.

The final percentages of emergence from the seeds treated with the mercurial and cuprous oxide series of dressings is given in Table XIII.

TABLE XIII.

% Emergence from Treated and Untreated Pea Seeds, var. The Lincoln.

Treatment.	%	Treatment.	%
Control	6	Control	8
Mercurial dressing	56	Cuprous oxide	76
M1	68	C1	80
M2	52	C2	86
M3	62	C3	82
M4	78	C4	76
M5	66	C5	78
M6	56	C6	80
M7	48	C7	78
M8	50	C8	82
M9	48	C9	78
M11	54	C10	84

As in the previous experiment, several of the mercurial dressings containing hormones gave a higher emergence percentage than the mercurial dressing alone. Of the three dressings containing naphthalene-acetic acid, M1, containing 5 parts per million of the acid, was the most effective. M2, containing 10 parts per million, and M7, containing 20 parts per million, did not induce so high an emergence as the mercurial dressing alone. This agrees with previous results which indicated that at high temperatures 10 parts per million of α-naphthalene-acetic acid incorporated in the mercurial dressing exceeded the optimum concentration. M4, containing 10 parts per million of naphthylidene-acetic acids, gave 78% emergence, 22% higher than that from the seed treated with mercurial dressing alone. The percentage emergence from seed treated with M1, containing 5 parts per million of hormone, was only 6% above that from

the mercurial dressing alone, while M9, containing 20 parts per million, gave a lower percentage of emergence than the mercurial dressing alone. Thus, with naphthylidene-acetic acids, 10 parts per million is probably the maximum concentration which may be employed with advantage in the mercurial dressing. Of the mixtures containing indolyl-butyric acid, M5, containing 5 parts per million, was the most effective. M9 and M11, containing mixtures of naphthalene-acetic and naphthylidene-acetic acids, did not give promising results.

Somewhat different results were obtained with the cuprous oxide series of dressings. It has already been pointed out that a mercurial dressing may cause a greater check to growth than a cuprous oxide dressing at high temperatures. This is borne out by the result of this experiment, in which the emergence from seed treated with cuprous oxide was 20% greater than that from seed treated with the mercurial dressing.

TABLE XIV.

% Emergence per day from Treated and Untreated Pea Seed, var. The Lincoln.

Treatment.	6th	7th	8th	9th	10th days.
Control	0	2	4	8	8
Cuprous oxide	4	24	60	68	76
C1	10	44	80	80	80
C2	12	56	76	86	86
C3	10	46	64	74	82
C4	4	36	70	76	76
C5	6	36	66	74	78
C6	12	54	76	80	80
C7	4	36	66	78	78
C8	8	46	72	76	82
C9	10	38	70	78	78
C10	8	38	78	84	84

The cuprous oxide dressings containing hormones gave only a slightly higher percentage of emergence than that obtained by treating the seed with cuprous oxide alone. It must be remembered, however, that the emergence from the cuprous oxide treated seeds, 76%, was very high, considering the conditions of the experiment, and was not likely to be readily improved upon. It was very noticeable that the emergence from the seeds treated with hormone-containing dressings was much more rapid than from the seeds dressed with cuprous oxide alone, as may be seen in Table XIV.

A surprising feature of these results was that there was such a slight difference in the effects of the different treatments and that the dressings containing the higher concentrations of hormones did not check the emergence of the seedlings.

Preliminary trials were also carried out to determine the effect of hormone-containing dressings on emergence from dwarf bean seeds. Seeds of the variety

Foremost were treated with talc, mercurial dressing, cuprous oxide and the corresponding hormone-containing dressings T1-T6, M1-M6 and C1-C6. The seeds were sown 1 in. deep, in boxes of soil similar to that used in the previous experiments with peas. The percentage emergence from the seeds subjected to each of the above treatments is given in Table XV.

In the talc series of dressings, although there is apparently some slight improvement in the percentage of emergence by the use of T1, T2, T3 and T5, little importance can be attached to this owing to the low percentage germination throughout.

The seeds dressed with the hormone-containing mercurial dressings M1, M3 and M5 gave 10 to 12% greater emergence than those treated with the mercurial dressing alone. Further, the seedlings emerged more rapidly and the plants were much more vigorous. The dressings M2, M4 and M6 had a similar but less marked effect.

Table XV.

% Emergence from Treated and Untreated Dwarf Bean Seeds, var. Foremost.

Treatment.	%	Treatment.	%	Treatment.	%
Control	10	Control	8	Control	10
Talc	8	Mercurial dressing	50	Cuprous oxide	30
T1	14	M1	62	C1	36
T2	14	M2	54	C2	40
T3	14	M3	60	C3	38
T4	10	M4	58	C4	38
T5	14	M5	62	C5	34
T6	8	M6	56	C6	50

The cuprous oxide dressings in which hormones were incorporated also gave better results than cuprous oxide alone, the dressings C2, C3, C4 and C6 being the most effective.

Too little is known about the effect of different seed dressings on dwarf bean seeds to suggest an explanation for the fact that in the mercurial series the dressings containing the lower concentrations of hormone, and in the cuprous oxide series those containing the higher ones tended to be most effective.

A second trial with beans was carried out with the variety Early Prolific, but did not yield any striking results. The experiment was carried out during hot weather with bright sunshine, and all the seedlings, including that of the controls, emerged rapidly. In less than fifteen days 86-92% of the seedlings emerged in all treatments and all of them continued to grow rapidly.

The trial with the variety Foremost indicates that hormone-containing dressings, especially those of the mercurial series, might be used with advantage

on dwarf bean seeds. It is realized that too much reliance must not be placed on the results of a single experiment and that further investigation of the effect of these dressings on a number of varieties of beans under various conditions must be made, before safe conclusions can be drawn.

FIELD TRIALS.

A number of field sowings were made of peas of the following varieties:—

Foremost.—Dressings of talc, T1 to T6, and cuprous oxide, C1 to C6, were applied to lots of 300 seeds each of this variety. The seeds were sown on May 8th under good conditions, the soil being warm and moist. Germination was rapid and there was no marked difference in the percentage of emergence with any of the treatments. It should be noted that this variety is usually sown at an earlier date, and that a seed dressing would not normally be used for so late a sowing. After emergence of the seedlings conditions became cold

TABLE XVI.

% Crop Weight of Treated and Untreated Pea Seeds, var. Foremost.

Treatment.	%	Treatment.	%
Talc	98	Cuprous oxide	72
T1	112	C1	104
T2	123	C2	99
T3	114	C3	93
T4	102	C4	89
T5	98	C5	70
T6	101	C6	89

and dry, and growth, especially of the plants from cuprous oxide treated seed, appeared to be checked. There was no difference in the time of flowering with any of the treatments. All marketable pods were picked on July 21st. The crop weights from each of the treatments are given in Table XVI as a percentage of the crop weight of the controls.

The seeds treated with talc dressings containing hormones, T1, T2, T3, produced a heavier crop than the control or the talc dressing alone. The crop from seeds treated with cuprous oxide alone was considerably lower than that from untreated seed. It should be emphasized, however, that under early sowing conditions the development of cuprous oxide treated seeds is less likely to be checked, and that as conditions are then more favourable to pre-emergence damping-off, any check would be more than compensated by the increased stand of plants. The use of dressings containing hormones resulted in crop yields up to 30% greater than those following treatment with cuprous oxide

alone. The dressing C1, containing 5 parts of α-naphthalene-acetic acid, was the most effective, but the use of C2, C3, C4 and C6 also resulted in greater crops.

Surprise.—A similar trial, using the same treatments and the same number of seeds, was laid down with the variety of Surprise on May 10th. Here, again, the percentage emergence was high with all treatments, varying from 82-88%. The pods were picked and weighed on July 21st. The crops weights, expressed as percentages of the crop weight of the controls, are given in Table XVII.

TABLE XVII.

% Crop Weight from Treated and Untreated Pea Seeds, var. Surprise.

Treatment.	%	Treatment.	%
Talc	101	Cuprous oxide	91
T1	110	C1	89
T2	124	C2	108
T3	100	C3	108
T4	120	C4	102
T5	97	C5	94
T6	84	C6	79

Increased yields were obtained from treatments with the hormone-containing dressings T1, T2 and T4. The most successful were T2 and T4, the dressings containing the higher concentrations (10 p.p.m.) of α-naphthalene-acid and mixed naphthylidene-acetic acids. T6, containing 10 p.p.m. of β-indolyl-butyric acid, tended to lower the yield.

The results obtained with the cuprous oxide series of dressings were not entirely consistent with those of the talc series. The yields from seeds treated with cuprous oxide alone were again slightly lower than those from the controls, although not so much as with variety Foremost. Use of the dressings C2, C3 and C4 resulted in the production of crops greater than in the controls, but the dressing C1, containing 5 parts per million of α-naphthalene-acetic acid, did not influence the yield. There was also a difference from the results of the talc series in that the dressing C3, containing 5 parts per million of mixed naphthylidene-acetic acids, gave better results than C4, containing 10 parts per million, while in the talc series, T3 was inferior to T4. The higher concentration of β-indolyl-butyric in the dressing C6 checked development as did the corresponding talc dressing T6.

The Lincoln.—In the first trial with this variety each of the treatments, the mercurial dressing, mercurial dressings containing hormones M1-M6, talc, and talc dressings containing hormones T1-T6, was applied to 600 seeds of the variety named. The seeds and the same number of untreated seeds were

sown on May 18th. Owing to the soil being rather dry, germination was slow. The final percentage emergences are given in Table XVIII.

It can be seen from this Table that there is a tendency for treatment with the hormone-containing dressings to give a slight but consistent increase in the percentage emergence as compared with the corresponding dressing without hormone.

TABLE XVIII.

% Emergence from Treated and Untreated Pea Seeds, var. The Lincoln.

Treatment.	%	Treatment.	%
Control	52	Control	53
Talc	51	Mercurial dressing	56
T1	56	M1	59
T2	59	M2	63
T3	56	M3	61
T4	56	M4	62
T5	57	M5	60
T6	56	M6	60

The pods were picked and weighed on August 14th. The crop weights, calculated as a percentage of the crop weights of the controls, are given in Table XIX.

Use of several of the hormone-containing dressings caused a marked increase in the yields. Of the talc dressings, T1, T3 and T5 were the most effective.

TABLE XIX.

% Crop Weight of Pea, var. The Lincoln.

Treatment.	%	Treatment.	%
Talc	100	Mercurial dressing	94
T1	123	M1	138
T2	98	M2	106
T3	114	M3	130
T4	76	M4	136
T5	97	M5	124
T6	117	M6	120

A surprising feature was the very low yield, 76%, from seeds treated with the dressing T4, containing 10 parts per million mixed naphthylidene-acetic acids, and also that treatment with the dressing T6, having a higher concentration of β-indolyl-butyric acid, was more successful than T5, having a lower concentration.

Treatment with the mercurial dressings containing hormones resulted in even greater increases in crop weights. The dressings M1, M3 and M4 were the

most effective. Here, again, the dressings containing the weaker concentration of α-naphthalene-acetic acid and the dressings containing the higher concentration of mixed naphthylidene-acetic acids were the most successful.

A second trial was carried out with this variety, using the same treatments and the same number of seeds as in the first. The seeds were sown on May 25th in dry, light, soil. Germination was slow, many of the seeds not germinating until after rainfall a fortnight after sowing. The final percentage emergences are given in Table XX.

TABLE XX.

% Emergence from Pea, var. The Lincoln.

Treatment.	%	Treatment.	%
Control	63	Control	56
Talc	64	Mercurial dressing	60
T1	68	M1	67
T2	67	M2	71
T3	66	M3	59
T4	63	M4	72
T5	70	M5	63
T6	68	M6	72

In this trial there again occurred slight increases in the percentage emergence from seeds treated with the hormone-containing dressings. This increase was most marked with the mercurial dressings M2, M4 and M6.

The pods were picked on August 29th and the yields, expressed as a percentage of the yield of the controls, are given in Table XXI.

TABLE XXI.

% Crop Weight of Pea, var. The Lincoln.

Treatment.	%	Treatment.	%
Talc	105	Mercurial dressing	112
T1	169	M1	196
T2	110	M2	166
T3	155	M3	168
T4	132	M4	168
T5	118	M5	167
T6	129	M6	145

The increases in yield obtained by use of the hormone-containing dressings were even greater here than in the previous trial. In both the talc and the mercurial series the dressings containing 5 parts per million of α-naphthalene-acetic acid, that is, T1 and M1, were outstanding, the yields being respectively

64% and 84% greater than those obtained by using the dressings without hormones. In both series the dressing containing the lower concentration of hormone was more effective than that containing the higher one.

Use of the dressings containing naphthylidene-acetic acids also resulted in considerably greater yields being obtained. In the talc series the dressing containing the lower concentration of hormone was somewhat more effective, but exactly the same yields were obtained from the seed treated with the mercurial dressings containing 5 and 10 p.p.m.

The results obtained from the dressings containing β-indolyl-butyric acid were more variable. In the talc series, T6, containing 10 parts per million, gave a rather better result than T5, but the yields were not nearly as high as those obtained by the use of the dressings T1 and T3. In the mercurial series, seeds treated with the dressing M5 gave the same yield as that obtained from seeds treated with M2, M3 and M4. The dressing M6, containing the higher concentration of β-indolyl-butyric acid, did not produce such a marked increase in crop weight.

DISCUSSION.

Although further investigation is needed, the results of the preliminary experiments described indicate that the application to seeds of dry fungicidal dressings containing growth promoting substances may be of considerable value.

In these experiments with several varieties of peas the development of the plants was markedly stimulated. The stimulation, however, appeared to be confined to vegetative growth since there was no noticeable difference in time of flowering.

Under laboratory conditions, no improvement in germination was obtained by applying these dressings to pea seeds. It must be pointed out that the seeds used germinated readily, and that the increased germination observed by Amlong and Naundorf (1) and others was obtained by treating poorly germinating seeds with solutions of auxins. The germination of one variety of pea (Eclipse) was reduced, under laboratory conditions, by treating the seeds with cuprous oxide ; this injury was not overcome by incorporation of hormones in the dressing.

Under normal field conditions mercurial and cuprous oxide seed dressings are not likely to exert any injurious effect, but greenhouse experiments showed that the development of certain varieties of peas tended to be checked by the use of mercurial dressings at high temperatures, and by treatment of the seeds with cuprous oxide when soil moisture was low. By incorporating growth-promoting substances with the dressings the check under these conditions was partly or entirely overcome, and the development of the plants was equal to or surpassed that of the untreated controls. In field trials during the summer,

when the soil was dry for a long period, the use of cuprous oxide and mercurial dressings alone tended to reduce the crops from three varieties of peas. Seeds treated with these dressings containing hormones gave higher yields which were almost equal to or were greater than those from untreated seeds. Thus, one advantage from the incorporation of growth-promoting substances with seed dressings appears to be that the possibility of injurious effects due to the dressings alone is much reduced.

More important still is the fact that when conditions were such that no check was observed from the use of cuprous oxide and of mercurial dressings alone, better results were obtained by treating the seed with the same dressings containing growth substances. In sterile soil in the greenhouse the rate of emergence of seedlings was accelerated and the plants had a greater dry weight after several weeks' growth when the seeds were treated with hormone-containing dressings. When seeds were sown in greenhouse soil heavily contaminated with damping-off fungi, those treated with hormone-containing dressings gave a higher percentage of emergence than those treated with the same dressings without hormones. In the single field trial, in which the seeds treated with a protective dressing alone gave a higher yield than the untreated seeds, still greater crops were obtained by using the same dressings containing hormones. The value of the hormones alone is shown by the fact that, in all the trials, increased yields were obtained by use of several dressings in which the hormones were incorporated with talc, which substance by itself had no effect on growth or yield.

Although the experiments indicate that advantages may be obtained by the application of growth substances to pea seeds, these substances cannot be used indiscriminately on all varieties and under all conditions. As Grace (4) found with wheat, different varieties show markedly different reactions to a single dressing. Moreover, the effect of one concentration of any of the substances applied to a single variety was different under different external conditions. Of the dressings used, no single concentration of any one of the growth substances gave an optimum reaction on all the varieties under the different experimental conditions. Indolyl-butyric acid, at the concentrations used, generally gave less favourable and more variable results than α-naphthalene-acetic acid and the mixed naphthylidene-acetic acids. These two acids were, on the whole, of approximately equal value, although some varieties gave a greater response than others. The information at present available indicates that there is no single concentration of either of these acids which gives the maximum stimulation at all stages of growth to all varieties and under all conditions. On the whole, the dressings containing 10 parts per million of these substances induced more rapid emergence in greenhouse trials than those containing 5 parts per million. On some varieties, however, 10 parts per million appeared to exceed the

optimum concentration, and this was confirmed by the results of the field trials with the variety The Lincoln described above. At present it appears that dressings containing 5 p.p.m. of α-naphthalene-acetic and mixed naphthylidene-acetic acids, although not producing the greatest response with all varieties and under all conditions, may safely be used for a number of varieties and may result in higher crop yields being obtained.

Further investigation is necessary in order to determine the effect of hormone-containing dressings under a wider range of conditions. It is hoped that the present studies may be extended to the use of these dressings on other crops. In order to be of practical value, attempts must be made to produce a dressing containing a concentration of hormones that may safely be applied to the seeds of the different varieties of various crops and be likely to produce a stimulating effect under a fairly wide range of growth conditions.

SUMMARY.

1. Dry seed dressings (mercurial and cuprous oxide), containing from 5 to 20 parts per million of α-naphthalene-acetic acid, mixed naphthylidene-acetic acids and β-indolyl-butyric acid were applied to the seeds of seven varieties of peas and two of dwarf beans.

2. In the laboratory, no acceleration of the rate of germination was obtained by the use of these dressings.

3. Partial failure of the seeds of one variety of pea to germinate under laboratory conditions when they were treated with cuprous oxide was not overcome by the incorporation of growth-promoting substances in this dressing.

4. In sowings in sterile soil in the greenhouse the rate of emergence from pea seeds was accelerated, and the dry weight of the seedlings after three weeks' growth was increased by treating the seeds with talc, cuprous oxide and a mercurial dressing, to all of which growth-promoting substances had been added.

5. The check to growth caused by mercurial and cuprous oxide dressings under certain greenhouse conditions was greatly reduced or entirely overcome by the incorporation of hormones with these dressings.

6. In greenhouse soil contaminated with damping-off fungi a higher percentage emergence from several varieties of peas and one of dwarf beans was obtained by treating the seeds with hormone-containing dressings than by the use of the same dressings without hormones.

7. In field trials, during the summer, the crop yields obtained from seeds of three varieties of peas treated with hormone-containing dressings were up to 80% greater than those obtained from seeds treated with the same dressings without hormones, or from untreated seeds.

8. There was a considerable difference in the response of different varieties to the dressings used. The effect of dressings containing growth-promoting substances also varied with different external conditions. No one dressing produced an optimum effect on all varieties and under all conditions. There was some indication that dressings containing 5 p.p.m. of α-naphthalene-acetic acid and mixed naphthylidene-acetic acids may safely be used on the varieties of peas and beans employed in these trials, and may cause considerable stimulation under some conditions.

ACKNOWLEDGMENT.

The writers are much indebted to the Horticultural Department, Messrs. Boots, Chemists, Nottingham, who supplied the mercurial and zinc oxide seed dressings and the growth hormones used throughout the experiments.

REFERENCES.

(1) *Amlong, H. U.* and *Naundorf, G.* Über einige praktische Anwendungen der pflanzlichen Streckungswuchstoffe. Der Forschungsdienst, 1937, **4**, 417.

(2) ——— and ———. Neue Wege der Pflanzenstimulation. Der Forschungsdienst, 1938, **5**, 292.

(3) *Cholodny, N. G.* Growth hormones and development of plants. Nature, 1936, **138**, 586.

(4) *Grace, N. H.* Physiologic curve of response to phytohormones by seeds, growing plants, cuttings and lower plant forms. Canadian Journ. Res., Sec. C., 1937, **15**, 538.

(5) ———. Physiological curve of responses to plant growth hormones. Nature, 1938, **141**, 35.

(6) ———. Effect of phytohormones on seeds damaged by formaldehyde and other disinfectants. Canadian Journ. Res., Sec. C., 1938, **16**, 319.

(7) *Kotowski, F.* Temperature relations to germination of vegetable seed. Proc. American Soc. for Hort. Science, 1926, **24**, 177.

(8) *McRostie, G. P.*, *Hopkins, J. W.* and *Grace, N. H.* Effect of phytohormones on growth and yield of winter wheat varieties. Canadian Journ. Res., Sec. C., 1938, **16**, 510.

(9) *Söding, H.* Die Wuchsstofftheorie in der angewandten Botanik. Angew. Bot., 1938, **20**, 407.

(10) *Thimann, H. V.* Hormones and the analysis of growth. Plant Physiology, 1938, **13**, 437.

(11) *Thimann, H. V.* and *Lane, R. H.* After effects of treatment of seeds with auxin. American Journ. Bot., 1938, **25**, 535.

(*Received* 23/10/39.)

BOOK REVIEWS

FRUIT JUICES AND RELATED PRODUCTS. By V. L. S. CHARLEY and T. H. HARRISON. (Technical Communication No. 11 of the Imperial Bureau of Horticulture and Plantation Crops, East Malling, Kent, England, 1939, pp. 104. 5s.)

The radical changes in the economic and social conditions of life generally during the present century have brought into prominence many problems affecting human nutrition. These have focussed more attention on dietetics and have had an incidental effect on the consumption of various forms of food and drink. As to the latter, as the authors have shown, a large and increasing demand for "soft" drinks has developed. So far as that group of beverages is concerned, a definite preference for the natural fruit products has become manifest. Citrus fruit juices and squashes have already established themselves firmly in popular favour, and now it would seem that the turn of apple juice has arrived, if the remarkable rate of expansion in production and consumption during the past decade—particularly in Germany and Switzerland—can be accepted as indicative of a genuine demand. Corresponding signs of growing popularity apply also to the unfermented juices of grapes, pineapples and tomatoes.

In a brief Foreword, Mr. Nevill Wright, Scientific Liaison Officer for the New Zealand Department of Scientific and Industrial Research and Chairman of the Executive Council of the Imperial Agricultural Bureaux, calls attention to the potential importance to the fruit industry of the establishment of profitable outlets for the utilization of that inevitable portion of the crop falling below the market grade standards, but otherwise edible and nutritious. "Liquid fruit" is commended by him to the fruit-growing industry of the British Empire as an outlet of high promise, surprisingly neglected hitherto within the Empire as a whole.

This neglect may have been due to some extent to the lack of a comprehensive book of reference in English on modern developments and operations in the fruit juice industry. Mr. Charley and Dr. Harrison have now met this need and have provided an authoritative contribution to the literature of the subject, including, as it does, the experience and summarized results of the extensive investigations of the first-named author and his co-workers at Long Ashton.

In their concise world survey of the existing unfermented juice industry, the facts recorded by them show its present value to fruit producers irrespective

of the high promise of its future development which, as they point out, must be largely contingent on the fulfilment of certain specific requirements essential for economic stability. Fickle as the public taste and demand notoriously are apt to be, the continued progress of the industry should be assured, even if only a fraction of the considerable claims made by various Continental practitioners and others, reported in the section on the nutritional and therapeutic properties of fruit juices, are confirmed by dieticians and the medical profession in general after wider experience and critical investigation.

The second and longer part of the Communication consists mainly of a detailed description of the methods of production of apple juice. It is this section which will be of special interest to manufacturers and prospective producers, for it contains an exceptionally complete account of the whole range of processing and the numerous accessory factors and considerations requisite for successful results, so far as present knowledge extends. The value of the text of this part is enhanced by the excellent series of illustrations supplementing the descriptive matter.

This account of the methods of apple juice production includes much applicable also to the preparation of other fruit products. For the latter, individually, this more general information is suitably supplemented in special sections which follow. In these, other unfermented fruit juices and the fermented products—wines, brandies and other distilled products, cider and cider vinegar—are briefly dealt with. The Citrus fruit juices are referred to mainly from the American point of view. This doubtless accounts for the statement that the most important preserved Citrus juice is grape-fruit, while orange and other juices of that group are still almost entirely sold in the fresh unpreserved state. In Great Britain, the importers of Citrus juices would not give grape-fruit juice that pre-eminence, popular as that product has proved in the mineral water trade recently: nor is the second part of the statement strictly accurate, for large quantities of raw orange, lemon and lime juices, suitably preserved for subsequent conversion into squashes, cordials and other products, have been shipped for many years from countries where these fruits are grown.

Other supplementary sections refer to fruit juice concentration, the freezing of fruit juices, spray drying of fruits and their juices, and various by-products of the industry.

Part II is usefully concluded by descriptions of relevant methods of chemical analysis and observations on the choice of metals for plant and equipment.

The publication is completed by the inclusion of a glossary, an extensive list of literature references and an index.

There are a few points where more precision might have been shown with advantage by the authors, even in a Communication containing so much valuable information in so few pages. For example, when referring to the

gelatine-tannin method of juice clarification, they specify the respective quantities of those two substances that are generally suitable, but omit to state which of the numerous "tannins" should be used.

Also, since a glossary has been deemed necessary in this Technical Communication, the addition of an explanatory note on the unfortunate ambiguity associated with the technicians' use of the terms "Aeration", "Carbonation" and "De-aeration" might prevent some confusion in the minds of non-technical readers.

These and other minor features open to criticism are slight, however, compared with the general value of this comprehensive and most interesting record of the recent developments of the fruit juice industry. Its authors can be congratulated on this addition of an indispensable contribution to the existing literature on the subject.

B.T.P.B.

PLANT HORMONES AND THEIR PRACTICAL IMPORTANCE IN HORTICULTURE. By H. L. PEARSE. (Technical Communication No. 12 of the Imperial Bureau of Horticulture and Plantation Crops, East Malling, Kent, England, 1939, pp. 88. 3s. 6d.)

When, a few years ago, synthetic growth substances became readily available, horticulturists promptly took the opportunity to put to practical test their reputed properties of stimulating root-formation. The considerable success obtained in many countries by investigators who have been able to facilitate and accelerate the vegetative propagation of many cultivated plants by treating cuttings with such substances has ensured a place for such methods in the routine operations of the industry. The positive response of certain fruit-stocks, such as Myrobolan B and Malling Pear stock C8, was first described by Dr. Pearse in this Journal two years ago (XV, No. 3, 1937), and the successful application of indolyl-butyric acid to soft-wood cuttings of apple (No. 1), cherry (F12/1 and others) and quince (A) stocks was reported by him later (East Malling Report 1938).

To Dr. Pearse has been entrusted by the Bureau the task of reviewing the progress made in this branch of applied plant physiology, and all readers of the Technical Communication under review that fulfils this trust will value his critical appreciation, knowing that it is based on practical experience.

The earlier pages of the Bulletin form a review of the factors previously known to influence root-formation in cuttings; there follows a clear summary of the work of thirty investigators who have used these substances in various experimental ways, work which has now led to the practical methods actually applied in the industry. As yet it has not been found that the time saved by the use of powders as carriers for the active substances compensates, with the

majority of plants, for the relative loss in efficiency as compared with the rather more troublesome use of solutions. The materials are available on the market in both forms.

A theoretical section is concerned with the way in which these substances work, the mechanism of induced root-formation. On this problem further investigations of a more highly technical nature must be carried out, for too little is yet known concerning the relationship of the chemicals to the underlying process of cell division which precedes root-formation. It appears that the chemicals may act as irritant drugs or as catalysts.

A feature valuable alike to the practical propagator and to the investigator is the long index of typical results obtained by the use of growth substances. Neatly overcoming difficulties in the presentation of data collected where different standards were employed, this index forms a valuable summary of information, showing the plants used, the season when cuttings were taken, concentration and other details of treatment employed and the results obtained ; but had all the concentrations been reduced to one standard method of expression, comparative reference would be easier. Although containing almost a thousand entries, the index makes no claim to be complete ; it could indeed be extended to include also several examples of the use of compounds quite recently found to be highly active.

Other possible uses of these substances in horticulture are considered. For example, it may in future be possible to encourage the development of roots from newly transplanted trees and to induce the development of (seedless) fruits, but it now appears less likely that the growth of whole plants may be stimulated by these substances which, after all, are root-forming stimulants primarily. The Bulletin concludes with a lengthy list of references to the original work on which it is based.

The index prepared by Dr. Pearse should be maintained and kept up to date by additional entries. It will function as a central register of plant propagation, and there appears to be no other such source of similar information. In issuing this Bulletin the Imperial Horticultural Bureau has performed a most useful task, and the suggestion that supplemental lists or indexes should follow in due time, merely expresses appreciation by asking for more.

M.A.H.T.

FUNDAMENTALS OF FRUIT PRODUCTION. By V. R. Gardner, F. C. Bradford and H. D. Hooker. Second Edition. (McGraw-Hill Publishing Co., Ltd., London, 1939, pp. xvi+788, 76 Figs. and 24 Tables. 30s.)

The first edition of this book appeared in 1922 and was reviewed by Mr. Bunyard in Vol. III of this Journal. At that time no work of the kind

had appeared, and there was urgent need for a book which would bring together the results of research and link them with established practice. This need was well met by the first edition and, although the book applied mainly to American conditions, it soon had a wide circulation and became a standard textbook. Since the date of its first appearance, however, research in pomology has progressed by great strides, and numbers of books which incorporate the more important of these advances have been published. While the fundamental theories of plant physiology remain largely unchanged, their applications to pomology have nevertheless undergone great revision and extension. To keep pace with this, a book such as that under review might have been expected to have been largely re-written. Unfortunately, this has not been done and, with one or two exceptions, it is merely a reprint of the original text with additions where necessary to include recent work. These extensions add 100 pages to the volume, although its actual dimensions remain nearly the same by the use of slightly thinner paper. Practically no deletion of material has been made and therefore most of the Tables and examples are still drawn from work which is now out of date.

Nor, unfortunately, is this the only criticism which can be levelled. The additions do not, by any means, cover even the most important of the recent work and newer conceptions. Three examples only need be given. In spite of the entirely new viewpoint given to physiology by the hormone concept of plant growth and behaviour, no mention whatever of the subject is made in the book. Considering the light that this conception may throw on such problems as propagation, vegetative growth, pruning and fruitfulness, the omission of all mention of the subject is surprising.

The other cases are, if anything, even more serious, in a book in which the approach is mainly through the viewpoint of nutrition and chemical composition. In the discussion of seasonal changes in the carbohydrates of the apple tree no mention whatever is made of the now classic work at Long Ashton, and the figures given are quoted from Hooker's results of 1920. Even the American work of Nightingale and Schermerhorn and others is not referred to. Finally, it is surprising to find no treatment of the work of Archbold and others on the chemical changes during ripening or of Kidd and West's discoveries on respirational trends and the onset of the climacteric.

In spite of these radical criticisms, however, the book still remains a mine of information, especially as applying to American conditions, and it contains much that is not to be found in other works. It is to be hoped that a third edition will appear, re-written in the light of modern knowledge and containing some reference to the fundamental work of investigators in this country, much of which is applicable in any country where fruit is grown.

R. H. STOUGHTON.

FRUIT GROWING. Edited by N. B. BAGENAL. (Ward Lock, London, 1939, pp. 399. 21s.)

This is the most comprehensive book on fruit growing that has been published for a long time. The chapters dealing with hardy fruits are exceptionally up to date and bring together the latest recommendations of the various Research Stations on the cultivation of the various fruits and the control of pests and diseases. In addition to this wealth of information, the book even includes notes on the cultivation of cranberries, sloes, bananas and pineapples! The book is written in an easy style, is exceptionally concise, and where full details are not given reference is made to sources of fuller information. The sixty illustrations and diagrams are excellent, although it is perhaps a pity that the eight coloured illustrations are not of pests and diseases, when they would be of greater practical value. A very full index is provided and the book as a whole is exceptionally free from printers' errors.

The general arrangement of the material follows the usual lines, with introductory chapters on soils, manuring, propagation, pruning, planting, marketing, exhibiting, and control of pests and diseases, and then the cultivation of particular fruits in alphabetical order.

The last chapters deal with fruits under glass, but they do not reach the same high standard as those on hardy fruit, and do not include in the same way the results of recent research. These chapters, also, are written almost entirely for the private gardener. It is unfortunate that the chapter on the use of frames does not mention Dutch lights, and the chapters dealing with the cultivation of cucumbers and tomatoes, although mentioning Damping-off, do not indicate the cause, or mention soil sterilization.

The large amount of tabulated information has enabled a great deal of detail to be included with regard to characters of varieties, the control of pests and diseases, times of flowering, etc., and also provides, in many cases, a summary for easy reference.

In conclusion, there is no doubt that this book will become a standard work on the subject, and it is hoped that it will be possible by means of future editions to keep it up to date. The book and the information it contains on hardy fruits can be recommended unhesitatingly to anyone who wishes for a concise treatise on the subject. The knowledge of fruit growing has increased so much in recent years that it is impossible even in a volume of 400 pages to include all the information available, but the essential information is included in this book in a concise, accurate and readable form.

C.E.H.